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**REGENERATION OF LODGEPOLE PINE
INFLUENCED BY SITE FACTORS AND
BURN INTENSITY IN THE GREATER
YELLOWSTONE AREA**

FINAL REPORT FOR RESEARCH AGREEMENT
#INT-90491-RJVA
"Regeneration of Lodgepole Pine Influenced by
Site Factors and Burn Intensity in the
Greater Yellowstone Area"
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FINAL REPORT

Regeneration of Lodgepole Pine Influenced by Site Factors and Burn Intensity in the Greater Yellowstone Area

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Part 1

FACTORS AFFECTING SEEDLING ESTABLISHMENT

INTRODUCTION

Fire is among the most important factors affecting the evolution, development, structure, and overall ecology of forest ecosystems in the Northern Rocky Mountains (Habeck and Mutch 1973, Houston 1973, Brown 1975, La Roi and Hnatiuk 1980, Romme 1982, Christensen et al. 1989). Mean fire return intervals range from a decade or two in low elevation *Pinus ponderosa* and *Pseudotsuga menziesii* forests to 300 years in high elevation subalpine forests of the region (Arno 1980, Houston 1973, Romme 1982, Romme and Despain 1989, Barrett 1994). *Pinus contorta*, the most widely distributed conifer in western North America, dominates mid-montane forests over much of this region, often forming monospecific stands (Wheeler and Critchfield 1985, Fahey and Knight 1986). Brown (1975) stated: "Fire, more than any other single factor, is responsible for the establishment and structure of most of the lodgepole pine (*Pinus contorta*) forests we know today. The literature abounds with evidence that lodgepole pine owes its prominence [in the region] to repeated fires ...".

During the summer of 1988, a complex of fires burned some 5.7×10^5 ha in the Greater Yellowstone Area (Christensen et al. 1989). Approximately 400,000 ha burned within the boundaries of Yellowstone National Park. Postfire assessments of burn extent and severity indicated that about 60% of the burns within the Park were canopy fires and about 35% were surface fires in forests; the remainder occurred in meadows, grasslands, or *Artemesia* steppe. These large fires were a consequence of extreme drought, persistent winds, and an extensive cover of highly flammable old-growth forests (primarily *P. contorta*) that had developed on the Yellowstone Plateau since

the last extensive fires in the early eighteenth century (Romme and Despain 1989).

In addition to their vast extent, the 1988 fires were characterized by their heterogeneity, which produced a complex mosaic of burn severities at spatial scales from a few meters to kilometers. This mosaic included areas of 1) severe crown fires where most foliage and fine branches were consumed, 2) "halos" of moderate severity in which trees were killed from surface fires or heat from adjacent crown fires, but needles, fine branches, and cones remained in the canopy, and 3) stands that were unburned or experienced only light surface fires (Christensen et al. 1989, Anderson and Romme 1991). The scale and complexity of these fires provided a unique opportunity to study postfire regeneration of *P. contorta* forests in relation to fire severity and a host of environmental factors (Christensen 1989, Knight and Wallace 1989).

Pinus contorta is among the fire-resilient species of pines, a group characterized by precocious reproduction, small seed, and, in the case of ssp. *latifolia*, a high degree of cone serotiny (McCune 1988). Cones bearing viable seeds are produced at an early age (5 to 10 years in open stands and 15 to 20 years in heavily stocked stands; Fowells 1965), but trees possessing the serotinous genotype produce only open cones until they are ca. 20 to 60 years old, after which a gradual transition to serotinous cones occurs (Perry and Lotan 1979, Lotan and Perry 1983). Older trees bear either serotinous cones or cones that open upon maturity (occasionally both), and both types of trees typically are found in the same stand (Muir and Lotan 1985b). *P. contorta* is a prolific seed producer, with estimates of annual yield ranging from 180,000 to 790,000 seeds/ha (Fowells 1965). Serotinous cones are retained in the canopy for many years; mature trees may hold well over 1,000 closed cones and the stored seed supply may number into the millions/ha (Clements 1910, Hellum

and Wang 1985).

P. contorta is typically regarded as a pioneer species, intolerant of conditions beneath a closed canopy but adapted for colonizing disturbed sites (e.g., Muir and Lotan 1985b, Fahey and Knight 1986). *P. contorta* is thought to germinate best on mineral soil or thin, disturbed duff (Lotan and Perry 1983, Parker and Parker 1983, Lotan et al. 1985). Organic seedbeds such as thick duff and litter may dry quickly and expose seedlings to drought, the primary cause of mortality in the first year (Lotan and Perry 1983).

Competition from herbaceous plants is thought to reduce seedling establishment (Fowells 1965, Stermitz et al. 1974, Parker and Parker 1983).

Differential patterns in lodgepole pine establishment after a fire may have long-lasting effects on stand structure, physiognomy, and dynamics. Because they are initiated by fire, lodgepole pine stands are often even aged (Moir 1969, Peet 1981). Stands of similar age, however, frequently differ in density, ranging from open stands of large trees to extremely dense, stunted "doghair" stands (e.g., Fowells 1965, Lyon 1984). Such differences are common in the Greater Yellowstone area. While conducting fire history studies in Yellowstone National Park, Romme and Despain (unpublished data) often observed adjacent *P. contorta* stands that differed in density, physiognomy, and successional stage, but the trees in both stands were the same age. The physiognomic differences were as great as one might see in stands that were 100 years different in age. Such differences probably reflect the initial postfire establishment of *P. contorta* seedlings (Lyon 1976), but the site-specific processes that result in dramatic differences in seedling densities are not well understood (Horton 1953, Arnott 1973, Lyon 1976, 1984, Lyon and Stickney 1976).

Our studies of postfire responses of *P. contorta* forests in Yellowstone National Park were initiated in 1989 with the establishment of paired plots in seven stands at four sites burned the previous year. One plot was in a severe canopy burn; the paired plot was within an adjacent "halo" where the trees were killed but the fire did not ignite the tree crowns. Fire severity had a strong influence on seedling density; at all seven sites, *P. contorta* seedlings were far less numerous in the canopy burn area (Anderson and Romme 1991). *P. contorta* seedling density was not related to density of potential competitors. We hypothesized that within site differences were a consequence of loss of seeds consumed or killed by the severe crown fire, whereas differences among sites were likely a consequence of the availability of seeds at the time of the fire, a function of the proportion of serotinous trees in the stand.

To investigate these hypotheses, we expanded the study in 1990 to include sites spanning the elevational range of *P. contorta* within Yellowstone National Park (Ellis et al. 1993). The principle objective of our study was to assess the relative importance of key variables in determining postfire establishment of *P. contorta* seedlings. We hypothesized that the most important variables would include 1) burn severity and size of the burned patch, 2) site characteristics such as geologic substrate and climate, 3) prefire stand characteristics including tree density, stand age, and proportion of trees having serotinous cones, and 4) postfire abundance of potentially competing herbs and shrubs. Specifically, we sought to test the following hypotheses:

1. Density of *P. contorta* seedlings will be lower in areas subjected to severe crown fires than in comparable areas subjected to fires of moderate severity (see Methods for description of burn severity classes).

2. Density of *P. contorta* seedlings in severe canopy burn areas will lower in areas that are more remote from nearest moderately burned, lightly burned, or unburned stand than in areas with a potential seed source in close proximity.
3. Across sites, density of seedlings in both severe and moderate burn classes will be positively correlated with the proportion of serotinous cones in the prefire stand.
4. Within a fire severity class, density of *P. contorta* seedlings will be inversely related to the abundance of potentially competing herbs and shrubs.
5. Survival of *P. contorta* seedlings will be density independent at low seedling densities and inversely proportional to seedling density at high seedling densities.

METHODS

Study Area.

Yellowstone National Park occupies some 9,000 km² in the northwest corner of Wyoming and adjacent areas of Idaho and Montana. The Park overlies a physiographically diverse landscape created by episodes of mountain building, vulcanism, glaciation, and erosion. Our studies were conducted primarily within the Central Plateaus Geov egetation Province (Despain 1990), where elevations typically are between 2,300 and 2,500 m. These high plateaus are underlain by Quaternary rhyolite, which weathers to a coarse, sandy soil having poor water holding capacity and low nutrient levels (*ibid.*). Most of the area is covered by *P. contorta* forests. Mean annual precipitation ranges from about 500 mm to over 600 mm (Despain 1987, Marston and Anderson 1991). Mean annual temperatures are near the freezing point (Marston and Anderson

1991). For further details on the physical environment and vegetation, see Despain (1990).

Fire Severity Classes

Extensive observations of burned areas in 1988 and 1989 indicated that three burn severity classes and one unburned class could be readily distinguished in the field (Anderson and Romme 1991):

Severe canopy burn: trees killed; needles and fine branches consumed by hot crown fire; most litter and duff on forest floor consumed.

Moderate burn: trees killed, usually by surface fire; needles in canopy not consumed; much litter and duff on forest floor consumed; needle fall produced litter layer on forest floor during 1989-1990.

Light burn: little tree mortality; light and scattered surface fire; most litter and duff not consumed.

Unburned: No evidence of recent fire.

These categories are strongly correlated with specific severity parameters including percent mineral soil, percent tree mortality, and total plant cover in the first postfire year (M. Turner and W. Romme, unpublished data); they also agree closely with burn categories that were developed from Landsat imagery and incorporated in the Park's geographic information system (GIS).

Permanent Plots and Sampling Regimes for Seedling Establishment and Cone

Abundance

In August of 1989 and June of 1990, we identified potential study sites where areas subjected to severe canopy burns were immediately adjacent to areas of moderate burn severity. Such areas were located by scanning burned sites from roadways and by examining burn severity maps on the Park's GIS. Moderate burns were readily distinguished by the persistence of rust-colored needles on the trees. Permanent plots were established at four sites in 1989

(see Anderson and Romme 1991) and at eight additional sites in 1990 (Figure 1). Permanent plots were chosen subjectively to represent the elevational range and diversity of forests dominated by *P. contorta* on the central plateaus. At the time of the 1988 fires, each site supported a mature, nearly monospecific stand of *P. contorta*. Locations and characteristics of the study sites are summarized in Table 1.

At each of the twelve sites, paired plots were established. One member of each pair was in a severe canopy burn; the paired plot was in an adjacent area subjected to a moderate burn. The paired plots were within 60 m of each other and were subjectively chosen to be as similar as possible in relation to aspect, slope, substrate, and prefire stand structure. Each plot consisted of a permanently-marked, 50-m transect.

In addition to the paired transects, a third transect was established in the nearest unburned or lightly burned stand at each site. These stands were used to estimate the proportion of serotinous trees in the area. Seedling density and stand structure data were also collected in these stands. To determine whether seed dispersal might limit seedling densities in severe burn areas, we established a "remote canopy burn" plot at ten of the study sites. This plot was at least 100 m from the nearest unburned or moderately burned stand that could serve as a seed source.

P. contorta seedlings and cones on the ground were counted in 50 contiguous 1-m² quadrats along each transect. This sampling protocol was chosen to minimize the number of permanent plot markers employed within the National Park (i.e., it was not necessary to mark each individual 1-m² quadrat) and because it was very time efficient. At transects where mean seedling densities fell below 0.5 m⁻², a strip transect of either 2 m or 5 m in width along the permanent transect line was inventoried. (This occurred

only on the canopy and remote canopy burn transects at Sites 1, 2, and 3). At two Sites (11 and 12) where seedling densities were extremely high, quadrats were sampled at every other meter along the baseline for a total of 25 1-m² quadrats. Seedlings of other species were noted when encountered but were generally rare and were not included in density calculations. *P. contorta* seedlings were recounted each summer through 1994 to monitor changes in seedling density.

Prefire Stand Characteristics and Stand Serotiny

Prefire stand structure at each study site was reconstructed by estimating age, density, and the frequency distribution of stem sizes for all transects. Stand age was estimated by coring the nearest canopy-dominant tree at 5 m intervals along each permanent transect (10 trees total). After sanding the cores, annual rings were counted using a dissecting microscope, and transect age was taken as the mean age of those 10 trees. Stand age for the entire site was estimated as the mean of the trees cored on all of the site's transects. The size distribution of trees in the prefire community was estimated by recording the diameter of a minimum of 100 trees with a diameter-at-breast-height (DBH) > 2.5 cm. Quadrat size for DBH data was usually 50 m x 20 m (0.1 ha along the permanent transect), but varied depending on stand density. Prefire stand density was estimated by tallying the trees used for DBH data and extrapolating to stems/ha. Size distribution within each site was assessed using DBH data to construct stem and leaf histograms for each transect (see 1991 Annual Progress Report). Binoculars were used to count the number of cones remaining in the crown of each stand dominant tree that was cored in the moderate and canopy burn transects.

The proportion of trees bearing serotinous cones at each site was estimated using binoculars to note the presence or absence of serotinous cones

on a minimum of 100 live trees at the unburned transect in each study site. Stand-structure data (density, age, diameter, serotiny) were collected at ten sites in 1990; data from Lewis River Canyon and Lewis Lake North (sites 3 & 4) were obtained in 1991.

To obtain a better estimate of the variability of serotiny within sites, we sampled additional unburned stands in the summer of 1991 (Ellis 1993). In these stands, which were usually within 1 km of the original, permanently marked unburned plots, we sampled a minimum of 100 trees along a transect line.

Cover Estimates

Coverage of vascular plant species and of non-plant entities such as rock, litter, mineral soil, burned litter/duff, charcoal, etc., were estimated in 1990 on all transects by point interception using a 0.5-m x 1.0-m point-sighting frame with 36 points (Floyd and Anderson 1982). Cover data were collected over the same 1-m² quadrats used for seedling density data. Vascular plant intercepts were tallied by species, and each cover category was converted to a percentage by dividing the total number of intercepts in that category by the total number of points sampled. Data were summarized by quadrat and by transect.

Statistical Analyses

Two sample, independent *t* tests were used to examine differences between moderate and canopy burn transects for lodgepole seedling densities, cones remaining in the crowns of dominant trees, and cones remaining on the ground at each study site. For these analyses, each 1-m² quadrat or each tree was treated as an independent sample. Although it might be argued that the contiguous quadrats were not independent, the assumption of independence seemed reasonable because the scale of a quadrat was large compared to that of

an individual cone or seedling, or even a clump of seedlings. This scale was also large compared to the scale at which characteristics of the soil surface in burned areas appeared to change (typically a decimeter or two). Thus it is likely that the distribution of seedlings or other entities sampled was essentially random with respect quadrat placement. For many comparisons, the differences were so large and so consistent across sites that statistical tests were unnecessary.

Correlation analyses were used to test for relationships between mean *P. contorta* seedling density in the moderate and canopy burn plots and the corresponding 1) proportion of serotinous trees in the stand, 2) mean number of *P. contorta* cones on the ground, and 3) mean number of cones remaining in stand dominant trees. Correlation analyses were also used to examine the relationship between seedling density and the other cover parameters for each burned transect. For these within site analyses, the m^2 quadrat was the sample unit.

RESULTS

Seedling Establishment. Seedling densities across the 12 study sites and burn severity classes were highly variable, differing by over four orders of magnitude from a low of 80 ha^{-1} at the remote canopy burn plot on the Solfatara Plateau to 1.9×10^6 at the moderate burn plot at Site 11 near the Madison River Bridge (Table 2). In general, seedling densities were highest at low and mid elevation sites and lowest at the high elevation sites. In all but four canopy burn plots there were more seedlings than required to replace the stand that burned, and in most cases the ratios of postfire seedling densities to prefire stand densities were much higher than one (Table 3). Across moderate burn plots, postfire seedling densities were not correlated with prefire stand densities ($P = 0.20$), but, for the canopy burn plots,

postfire seedling densities were positively correlated density of the stand that burned ($r = 0.58$, $P = 0.047$). This indicates a tendency for dense stands to be replaced by dense stands and visa versa, at least in severely burned areas.

Densities of *P. contorta* seedlings in 1990 were from 4 to 24 times higher in moderate burn plots than in paired canopy burn plots, and the differences were highly significant ($P < 0.005$) at all 12 study sites (Figure 2). With the exceptions of Sites 8 and 11, seedling densities were two- to seven-fold lower at the remote canopy burn plot than at the canopy burn plot (Table 2). These data indicate that establishment of *P. contorta* seedlings in canopy burn plots was enhanced by dispersal of seeds from the adjacent moderately burned stand. The high seedling densities at the remote canopy burn plots at Sites 8 and 11 probably reflect high levels of serotiny in the stands that burned; in both cases the proportion of serotinous trees was near 50% (Table 1).

Cone Abundance. With the exception of Site 6 ($P = 0.30$), the mean number of cones on the ground in moderate burn plots was significantly higher than that in canopy burn plots ($P < 0.005$ in all 11 cases; Table 2). Across the moderate burn plots, *P. contorta* seedling density was strongly correlated with the number of cones on the ground ($r = 0.92$, $P < 0.001$). That correlation across canopy burn plots was not as strong ($r = 0.53$, $P = 0.07$), but still indicates that the relationship held for areas subjected to severe crown fires. The numbers of cones on the ground in the remote canopy burn plots were generally comparable to that of the canopy burn plots (Table 2).

Numbers of cones remaining in the crown of ten canopy dominant trees at the moderate and canopy burn plots were highly variable, and it was difficult to get accurate counts on trees that had more than 300 cones. Variability

among trees was especially high in areas where trees with and without serotinous cones were sampled. Trees having the serotinous trait may have a thousand or more cones in the crown. As a consequence of the high variability among trees, significant within site differences were found at only four sites (Table 2). Three of these were high elevation sites where no trees had serotinous cones. Despite the within site variability, there is a clear trend across sites. The mean number of cones per tree was higher in the moderate burn than in the canopy burn plot at 11 of the 12 sites, and, taking these values as a site estimate, the number of cones in crowns of moderate burn trees was significantly higher than that in canopy burn trees across sites ($P = 0.002$, Wilcoxon signed-ranks test).

Serotiny. The proportion of serotinous trees in the unburned stands at the 12 sites ranged from 0 to 48% (Table 1). Serotiny was highest among the low and mid elevation sites; no serotinous trees were found at four sites, three of which were at high elevations (Table 1). Prefire stand serotiny was strongly correlated with \log_{10} seedling density of both moderate and canopy burn plots (Figure 3). Numbers of cones on the ground in burned plots were weakly correlated with stand serotiny ($r = 0.58$, $P = 0.049$ and $r = 0.54$, $P = 0.069$ for moderate and canopy burn plots, respectively).

In 1991, we inventoried additional unburned stands within the general vicinity of nine of our sites to assess variation in local serotiny levels. At four sites, large differences in the proportion of serotinous trees were found between the original stand surveyed and another stand within 1 km (Table 4). No serotiny was noted in the original unburned stand at Site 5, but serotiny was 14% at Norris Junction, approximately 1 km to the west. At Site 6, serotiny fell from 48% at the original unburned plot to 17% in a stand less than 1 km north. At Site 9, where serotiny was 4% in the original plot, a

stand on the ridge less than 1 km east had 28% serotiny. And, serotiny rose from 15% in the unburned plot at Site 10 to 63% within 1 km. Variation among stands was much lower at Sites 7 and 8 (Table 4). We conducted extensive searches of unburned stands in the vicinity of the three high elevation sites where no serotinous trees were found in the original unburned plots. No serotinous trees were found in any of the three areas. That serotiny is very rare at such high elevation sites was apparent from sampling on the Solfatara Plateau where searching every unburned stand within 3 km of the study site failed to produce a single tree with serotinous cones (Ellis 1993).

Vascular Plant Cover. Total cover of vascular plants ranged from 1% to 34% on moderate burn plots and from 0 to 18% on canopy burn plots (Table 5; see Appendix 1 for species coverages at individual sites). With the exception of Site 2, vascular plant cover was lower on canopy burn plots than on the paired moderate burn plots. Richness of vascular plant species was considerably higher on moderate burned plots vs. canopy burn plots, with the exceptions of Sites 9 and 10 (Figure 4). None of these results was surprising; they reflect differences in plant mortality as a consequence of burn severity. However, we were surprised that correlation analyses of within-site data failed to show any consistent relationship between the presence of *P. contorta* seedlings and cover of vascular plants, litter cover, or any other cover parameter listed in Table 5. Across moderate burn transects, *P. contorta* seedling densities were not correlated with cover of other vascular plants or any other parameter ($P > 0.20$ in all cases). Across canopy burn transects, *P. contorta* densities were positively correlated with cover of other plant species ($r = 0.75$, $P = 0.006$) but not with any other cover parameter ($P > 0.40$ in all cases). The positive correlation probably reflects patterns of mortality of both *P. contorta* seeds and vegetative

structures of other species in areas subjected to severe canopy burns. Where fire intensities were lower, more understory plants as well as *P. contorta* seeds survived.

Prefire Stand Structure. It seemed possible that prefire stand age or structure could explain why crown fires occurred in some areas but not in adjacent halos of moderate burn severity. If this were the case, we would have expected consistent differences across sites in age or density between moderate and canopy burn plots. The sites generally fell into two age groups; in one, stands were initiated between ca. 170 and 200 years ago, and in the other, stands were from just under 100 to ca. 130 years old. With the exceptions of Sites 1 and 10, stand age was very similar across the three or four permanent plots at each site, indicating that the stands that burned as well as adjacent stands were even-aged and initiated at about the same time (Figure 5). The sign of the difference in age between moderate and canopy burn plots was not consistent. Even at Sites 1 and 10, there was little difference in age between the moderate and canopy burn plots. However, stands at those two sites were uneven aged, indicating that the forest had gradually filled in over the last two centuries.

Stand densities within plots were more variable than were stand ages, but again there was no consistent pattern in the sign of the difference in density between moderate and canopy burn plots (Figure 6). At three sites, 1, 3, and 12, there were substantial differences in density between moderate and canopy burn plots; at the remaining nine sites, those densities were very similar. While it is possible that lower density may have made the moderate stands less likely to crown at Sites 1 and 3, burn characteristics at those high elevation sites were similar to those at Sites 2 and 4, where prefire densities among plots were nearly identical. At Site 12, density of the

moderate burn stand was higher than that of either canopy burn plot, which is the opposite of what one would predict if differences in stand density were to account for fire behavior. We conclude that neither age nor structure of the stands that burned could account for differential burn severity or for differences in the various postfire parameters measured in this study (Ellis et al. 1994).

Mortality and Recruitment. Our sampling design for seedling densities did not enable us to track the fates of individual seedlings. However, repeated samples from the quadrats on the permanent transects provide estimates of the annual rate of density change, which reflects both mortality and recruitment (Table 6). Relatively high rates of decrease in seedling density were observed at only three sites, Mt Washburn, Lewis Lake, and Indian Creek. High mortality at Mt. Washburn was a consequence of severe erosion that deposited debris on the areas sampled, especially the moderate and remote transects. Erosion on the steep slope may have contributed to seedling mortality on the moderate plot at Indian Creek as well. Aside from those three sites, rates of density change were generally modest (Table 6). Rates were negative at most of the moderate burn plots, indicating that mortality was greater recruitment, but at about half of the canopy and remote canopy burn plots, recruitment was sufficient to offset mortality. The estimate of a 35% annual increase in density at Site 1 probably has a large error associated with it because of the very small number of seedlings present within the area sampled. Nevertheless, we have witnessed continued recruitment at that and most of the other canopy burn plots. Overall, the results indicate that mortality rates have been quite low at most of the study sites. This conclusion is supported by casual observations in the field: we encountered very few dead seedlings as we conducted the annual inventories.

There was no indication in the data that mortality was density dependent. The highest rates of density decrease were observed at sites where seedling densities were quite low. Sites with the highest seedling densities (Sites 7, 8, 11, 12) all had modest rates of density change.

An additional estimate of rates of density change was available for three study sites where plots were established to study the effects of competitors on *P. contorta* seedling growth (see Part 2). At each site, the total number of *P. contorta* seedlings were recorded in 1991 and 1993 in each of ten 1-m² quadrats of the "control" and "interspecific competitors removed" treatments. Counts for the ten quadrats were pooled to estimate rates of density change (Table 7A). These rates, ranging from 0 to -4.3%, are comparable to those from the seedling density data (Table 6). That annual mortality rates were only -2 to -3 % for plots where *P. contorta* seedling densities range from 120/m² to 150/m² (Table 7A) is surprising.

Finally, we were able to estimate mortality directly from loss of marked seedlings in our competition study plots. Four seedlings were marked in each of ten 1-m² quadrats per treatment. Again, we limit our analyses here to those plots in which the densities of *P. contorta* seedlings were not manipulated, the "control" and "interspecific competitors removed" treatments. Mortality rates for the 80 marked seedlings were below 2% per year at all three study areas. Only nine of 320 seedlings were lost over four growing seasons! These data confirm that mortality rates have been low over the first six postfire years, even in extremely dense stands of seedlings.

DISCUSSION

Effects of Fire Severity on Recruitment of Pinus contorta Seedlings

Our data clearly show that two factors are of primary significance in determining postfire densities of *P. contorta* seedlings, fire severity and the

level of stand serotiny. Both factors affect postfire seed supply. The data are consistent with the hypothesis that seedling densities will be lower in areas subjected to severe crown fires than in areas that received only surface fire, confirming the results of our initial study (Anderson and Romme 1991) over a broader range of site conditions. Our data are consistent with the scenario presented by Brown (1975) based on studies by Muraro (1971, as cited by Brown 1975): A hot surface fire with some crowning kills all of the trees and opens serotinous cones, releasing abundant seed on a mineral seedbed, which results in a dense stand. Where fire intensity is sufficient for a severe crown fire, however, some seeds are either consumed or exposed to lethal temperatures, the supply of viable seed is limited, and a relatively low density stand develops. Thus, Brown (1975) acknowledged that crown fires may destroy large quantities of stored seed, but noted that "The extent to which high-intensity fires reduce quantities of viable seed is speculative."

Our data provide quantitative estimates of the extent to which viable seed may be lost in a crown fire. Across the twelve sites, the average reduction of seedling density on canopy burn plots relative to that on the paired moderate burn plots (Table 2) was 84% (S.E. = 1.83; range: 75 to 96%). That the proportional reduction on canopy burn plots relative to their moderate burn counterparts was nearly constant across plots is shown by the parallel slopes of the relationship between \log_{10} seedling density and percentage of serotinous trees in the stand (Figure 3). Assuming that conditions for seedling establishment were comparable on the moderate and canopy burn areas, which seems reasonable given the results of a companion study of seedbed characteristics (von Dohlen et al., manuscript), we suggest that a severe crown fire is likely to destroy about 80 to 88% (95% C.I.) of the seed stored in a lodgepole forest canopy relative to the proportion that

survives a hot surface fire. Nevertheless, our data show that if there is even a modest proportion of serotinous trees in the stand, the seed supply will be adequate to replace the stand under severe crown fire conditions. "Overstocking" can be thought of a consequence of selection for sufficient storage and protection of seed to insure regeneration of a stand under such conditions.

The conclusion that severe crown fires may effect the simultaneous release and destruction of much of the seed rain in *P. contorta* runs counter to several previous studies. Muir and Lotan (1985a) suggested that few seeds are burned by stand-replacing fires, and LaMont et al. (1991) argued that evidence of heat-killed canopy stored seeds in serotinous species is extremely rare and occurs only in what they cite as the unusual event of cone ignition. However, despite evidence showing high survival of *Pinus* seeds in thickly scaled serotinous cones exposed to 250°C for 5 seconds (LaMont et al. 1991), there is ample evidence that exposure of seeds to temperatures in excess of 80°C will markedly decrease viability (Lotan 1975b, Knapp and Anderson 1980, Hellum and Wang 1985). Seed losses do not just result from ignition; the severity and duration of thermal stress are probably more important. The differences in numbers of cones on the ground and cones remaining in the canopy (Table 2) indicate some consumption of cones by crown fires. That there was not a more apparent difference in numbers of cones remaining in the canopy (significantly higher in the moderate burn plot at only four of 12 sites) suggests that much seed mortality may in fact result from lethal temperatures rather than direct consumption by the fire.

Effects of Serotiny on Postfire Recruitment

Lotan (1975b) and Muir and Lotan (1985a, b) suggested that differences in prefire serotiny levels could be a major factor determining postfire

seedling densities and could also provide an index of seed availability. Our data provide strong support for those suggestions. We found that densities of *P. contorta* seedlings increased exponentially with increasing levels of serotiny, and the relationship held with a similar slope for both moderate and canopy burn plots (Figure 3). The strength of the correlations indicate that from 45 to 50% of the variation in seedling density could be accounted for by variation in stand serotiny. That the relationship is exponential means that relatively small differences in serotiny will be magnified in terms of seedling density. Our data (Table 4) are consistent with those of others (e.g. Lotan 1975b, Lotan et al. 1985, Muir and Lotan 1985a) which show that there can be substantial differences in the level of serotiny over relatively short distances. Tinker et al. (1994) surveyed serotiny in nine patches that burned in the Yellowstone fires. They reported that serotiny was most variable at intermediate scales (1 - 10 km) and relatively homogeneous at fine scales (< 1km). For most of our sites, the unburned stand in which we inventoried serotiny was adjacent to the moderate burn plot, so we are confident that the estimate would hold for the burned plots. At a few sites, however, (e.g., Sites 9 and 10) the nearest unburned patch was 0.1 km or more from the moderate and canopy burn plots. In such cases, local variation in serotiny could have been important and may have contributed to the variability in seedling densities not accounted for by our serotiny samples.

The proportion of serotinous trees in a stand appears to depend strongly on the nature of the most recent disturbance (Perry and Lotan 1979, Muir and Lotan 1985b). Muir and Lotan (1985b) found that stands originating after fire had a large percentage of trees with serotinous cones, whereas stands originating after other disturbances had a large proportion of open cones.

The second factor that appears to be important in determining the level

of serotiny is elevation, probably operating through its effects on fire frequency. Lotan (1967), Brown (1975), Muir and Lotan (1985a, b), and Lotan et al. (1985) have suggested that the proportion of serotinous trees decreases with elevation in the Northern Rocky Mountains. Muir and Lotan (1985b) found no correlation between elevation and level of serotiny, but all of their study sites were below 2300. Lotan (1968) found that serotiny was lower on the high elevation Moose Creek Plateau (adjacent to the western boundary of Yellowstone National Park) than in nearby stands at lower elevations in the Island Park area. Tinker et al. (1994) reported a strong negative correlation between incidence of serotiny and elevation for 13 stands in Yellowstone, and, as we also found, serotiny levels were very low at elevations above 2300 m. For our 12 sites, a negative correlation between % serotinous trees and elevation was marginally significant ($t = 2.03$, $P = 0.07$); however, inclusion of four additional sites where we inventoried seedling densities and serotiny (data not shown) resulted in a significant relationship ($r^2 = 0.31$, $t = 2.53$, $P = 0.024$). There can be little doubt that the incidence of serotiny decreases with elevation in the Greater Yellowstone area.

We postulate that the low incidence of serotiny in higher elevation forests is a consequence of long fire intervals. The high elevation forests in Yellowstone may have mean fire intervals of over 300 years (Romme 1982, Romme and Despain 1989). Stands may be uneven aged, as occurred at our Site 1, indicating that they have gradually become restocked since the last fire or that there has been recruitment of young trees as gaps have been created by the deaths of old individuals. Mature spruce-fir forests in Yellowstone typically have a sizable complement of uneven aged *P. contorta* that have colonized gaps created as old lodgepoles have died (D. Despain, personal communication; see also Perry and Lotan 1979, p. 966). We propose the

following scenario to account for the low incidence of serotiny at high elevations: Long fire intervals often result in old-growth forests in which abundant gaps are created as old *P. contorta* individuals succumb. Such gaps are, in turn, colonized by seedlings from open cone trees. Under such conditions, there would be strong selection for the open cone trait, and stands developing under such conditions would have a low level of serotiny. When such stands are subjected to infrequent but intense wildfire, as occurred in 1988, resulting seedlings densities would be very low, as documents by Tinker and Romme (1994) and this study. Again, there would be strong selection for the open cone trait to repopulate sparsely colonized areas.

Perry and Lotan (1979) discuss the conditions necessary to maintain the cone polymorphism in *P. contorta*, assuming that cone serotiny is under one-locus, two-allele control. They note that where selection is strong, as in the case of fire selecting for serotiny, fixation of one allele is expected to occur rapidly. In describing potential conditions that would select for open cones, they describe a situation similar to that which we have proposed: "Even in the absence of low intensity fires, second-generation lodgepole pine often become established in small openings within the parent stand." These second-generation trees, established from open cones, would then be the primary source of seed when the stand is destroyed by a severe crown fire. Perry and Lotan note that this situation requires a longer interval between intense crown fires "than is generally thought to be the case." However, such long intervals are the case in the high elevation forests of the Yellowstone Plateau, and we think it likely that continued strong selection for the open cone phenotype could result in fixation of that allele despite the fact that such forest are occasionally subjected to severe fires.

Effects of Interspecific Competitors on Establishment of Pinus contorta

Seedlings

Our data do not support the hypothesis that establishment density of *Pinus contorta* will be inversely related to abundance of potentially competing herbs and shrubs. The lack of any significant negative correlation between seedling density and cover of other vascular plants (Table 5) confirms our earlier impression that interspecific competition had little, if any, impact on *P. contorta* seedling establishment (Anderson and Romme 1991). Fine-scale, intensive sampling at three of the study sites by von Dohlen et al.

(manuscript) showed that *P. contorta* seedlings became established on a wide variety of substrates and that associations with other vascular plants were generally positive or neutral. They found only one negative association, that between *P. contorta* seedlings and *Calamagrostis rubescens*. Other studies indicate that *C. rubescens* can retard conifer regeneration when it establishes early after a fire (Stahelin 1943, Lotan and Perry 1983). The negative association recorded by von Dohlen et al. (manuscript) was of little consequence in terms of seedling establishment, however. It occurred at Site 11's moderate burn plot where seedling densities averaged 196 m^{-2} ! We conclude that presence of potential interspecific competitors generally did not significantly affect establishment of *P. contorta* seedlings on areas occupied by lodgepole pine and burned by the 1988 Yellowstone fires.

Post-establishment Changes in Density of Pinus contorta Seedlings

Data from the Sleeping Child fire (Lyon 1976, 1984) suggest that we might expect an annual seedling mortality of about 6% over the first decade. Seedling attrition on most of our plots has been considerably less than that (Tables 6, 7). Lyon (1984) indicated that attrition would be higher in areas having higher seedling densities. Our data, spanning the first six postfire years, provide no support for the hypothesis that seedling mortality is

density dependent, despite the fact that two of our sites have seedling densities two and five times higher than the highest densities reported by Lyon.

Additional recruitment has been documented on areas where seedling densities are very low. Turner et al. (1994) showed that areas subjected to severe crown fires in 1988 were generally in close proximity to unburned or moderately burned areas that could serve as a source of *P. contorta* seeds. They point out that even the major "fire runs" of 1988 were long and narrow, so that "even the most extensive patches of crown fire were lined by less severely burned and unburned forests." Fowells (1965) suggested that *P. contorta* can restock clearcut areas that are within about 60 m of uncut forest. Using that appraisal of dispersal limitation, Turner et al. (1994) estimate that 30% of the crown fire area resulting from the 1988 Yellowstone fires would be within the seed shadow of living *P. contorta*. Fowells' (1965) distance estimate is based on silvicultural restocking requirements, however. Some seeds undoubtedly will be transported longer distances, resulting in the gradual "filling in" of high elevation areas where seedling densities are very low, as we have suggested earlier. Thus, we should expect additional recruitment at our high elevation sites.

We rarely saw evidence of animal damage to seedlings at any of our study sites. Evidence of pocket gophers (*Thomomys bottae*) was common at most sites, but it is clear that they did not cause much seedling mortality. Lotan and Perry (1983) noted that trampling damage by large herbivores such as cattle is a major cause of mortality of young *P. contorta*. Given large populations of bison and elk in Yellowstone, we expected that trampling might cause significant mortality in some areas. However, that was not the case, even at Site 7 where use of the area by both bison and elk was heavy. There was no

evidence of browsing on seedlings, probably, as Lotan and Perry (1983) pointed out, because seedlings are covered by snow during the season when ungulates feed on conifers.

Effects of Fire Severity and Levels of Serotiny on Landscape Heterogeneity

Although vast expanses of Yellowstone National Park will be dominated for many decades by a single cohort of *P. contorta* that became established in 1989 or soon thereafter, those developing forests certainly will not be homogeneous. Fire severity, incidence of serotiny, and local environmental conditions have interacted to produce stands that differ markedly in density and rates of seedling growth (see Part 2). It is likely that the resulting differences in stand and community structure will persist on the landscape until the next stand-replacing fires occur, as was indicated by Lyon's (1984) assessment of postfire succession over 21 years in similar *P. contorta* forests. The 1988 fires demonstrated that extensive fires during a single severe season can create complex patterns and tremendous variety within forests dominated by a single tree species.

Part 2.

FACTORS INFLUENCING GROWTH OF *PINUS CONTORTA* SEEDLINGS

INTRODUCTION

Densities of *P. contorta* seedlings that established after the 1988 Yellowstone fires varied by four orders of magnitude across different burn severity classes at 12 study sites (see Part 1, Table 2), but in the vast majority of cases, seedling density was far higher than the density of trees in the stand that burned. For example, at plots in areas of moderate burn severity (see Part 1, Methods, for definitions of burn severity classes), the ratios of postfire seedling densities to prefire stand densities ranged from 7.7 to 400 (Table 3). Clearly, significant thinning will occur in many of these stands as they mature. We postulated that there would be two stages of competition and thinning in *P. contorta* stands in which seedlings become established at relatively high densities. In the first stage, competition for below-ground resources would be critical, and we expected that rates of seedling growth would be density dependent. Further, as explained below, we predicted that seedlings with fewer close neighbors would become stand dominants during this stage. Lyon's (1976, 1984) research on Montana's Sleeping Child Fire indicated that the eventual stand-dominants would be apparent among *P. contorta* seedlings by the tenth postfire year. When these dominant saplings reach sufficient size for their crowns to begin to overlap, competition for light will become increasingly important. We anticipate that this second stage of competition will be characterized by high mortality of young trees that have been overtapped. The objective of the research reported here was to examine early seedling growth in an effort to identify those factors that might determine which seedlings become stand dominants.

There is little doubt that crowded neighborhoods can affect an individual plant's growth and performance. The competitive effects within a neighborhood are a consequence of the number of neighbors, their size, and their proximity to a target plant. Plants that establish first or that encounter fewer neighbors may monopolize local resources and grow more rapidly than those that establish later or that are found in more crowded neighborhoods (Shainsky and Radosevich 1992). Given these arguments, we predicted that rates of seedling growth would be inversely proportional to both the number and proximity of neighbors.

It is generally held that intraspecific competition will be more intense than interspecific competition because conspecific neighbors have similar physiology, phenology, and morphology (Barbour et al. 1980). Strong effects of intraspecific competition have been demonstrated in crowded stands of pines, including reduced stem diameter (Oren et al. 1987), retarded hydraulic and canopy development (Keane and Weetman 1987), and decreased water use efficiency (Drivas and Everett 1988).

Variation in spatial pattern potentially can have a large influence on the effects of intraspecific competition (Huston and DeAngelis 1987). For example, if seedlings were evenly distributed, all individuals would have the same number and proximity of neighbors, and all would tend to grow at a similar rate (assuming a homogeneous environment), and there would be little change in the size distribution with time. In contrast, if the distribution of seedlings were random or clumped, some individuals would have many neighbors while others would have few. Those with few neighbors would likely grow more rapidly, and we would expect to see a change in the size distribution as a few isolated individuals became dominant (see Figure 3 in Huston et al. 1988). Our initial samples of *P. contorta* seedling density

demonstrated that seedling distributions were strongly clumped (Anderson and Romme 1991); thus, we predicted that differences in the intensity of intraspecific competition would lead to variation in size among seedlings, with more isolated individuals growing more rapidly than those in crowded neighborhoods.

We also might expect that interspecific competition would affect early seedling performance. Grasses, sedges, and forbs frequently are cited as formidable competitors with *P. contorta* seedlings (e.g., Brown 1975, Lotan and Perry 1983, Lotan et al. 1985, Powell et al. 1994). Interspecific competitors can reduce water use efficiency (Carter et al. 1984, Stuart et al. 1989), survival (Stermitz et al. 1974, Peterson and Maxwell 1987, Powell et al. 1994), and stem diameter and height (Chapman 1945, Powell et al. 1994) of pine seedlings.

Two additional factors may result in differential performance among seedlings, genetic variability and environmental heterogeneity. Given the micro-scale heterogeneity of the postfire environment, we might expect significant differences in resource availability among microsites. Thus, the performance of an individual seedling is likely a complex a function of its genotype, the resources available in its microhabitat, and the number and kinds of competitors present. Our studies were designed to assess the importance of intraspecific and interspecific competition within this matrix of effects.

METHODS

See Part 1 for a description of the study area, locations of sites (Figure 1), general characteristics of sites (Table 1), prefire stand structure and postfire seedling densities at the study sites (Table 2), and descriptions of fire severity classes (Methods).

Effects of Fire Severity on Seedling Growth. To compare growth of *P. contorta* seedlings between moderate and severe burn plots, we measured stem diameter and height of seedlings at six sites in September of 1991. Diameter and height were measured on 50 seedlings in the moderate and severe burn plots at Sites 7, 8, and 11 and on 25 seedlings in each burn category at Sites 9, 10, and 12. Seedlings were selected systematically along a 50-m transect laid parallel to the permanent transect by sampling the seedling closest to each meter mark ($n = 50$) or every other meter mark ($n = 25$). Stem diameter was measured at ground level to the nearest 0.01 mm. Seedling height was measured to the nearest mm from the ground to the tips of the longest needles, holding the needles upright parallel to the stem. At Sites 7, 8, and 11, aboveground biomass was determined on all seedlings measured. Seedling were clipped at ground level, dried in an oven at 75°C, and weighed to the nearest 0.1 g.

To obtain additional data for examining seedling size class distributions, 200 seedlings were measured in the moderate and severe burn plots at Sites 7, 9, 10, 11, and 12 in June of 1992. Diameter and height were measured as explained above on the closest seedling in each of four quadrats corresponding to each meter mark along the 50-m permanent transect.

Two sample, independent *t*-tests were used to examine differences in height, diameter, and aboveground biomass between burn categories for each site. Simple linear regression was used to examine the relationships between aboveground biomass and either seedling height or diameter. Within sites, regression coefficients for biomass vs. height or diameter for seedlings moderate and severe burn plots were compared with a *t* statistic. Across sites, the slopes of these relationships were compared using GLM ANOVAs.

Quantification of Competitive Neighborhoods. In August and September of

1991, we assessed the abundance of potential competitors in the immediate neighborhood of each of 25 target seedlings in the moderate and severe burn plots at Sites 7, 8, 9, 10, and 12. Target seedlings in each plot were those nearest the tape at odd-numbered intervals along the permanent 50-m transect. Excavations at several sites indicated that the roots systems of three-year-old *P. contorta* seedlings rarely extended beyond about 0.3 m horizontally, so we limited our sample of potential competitors to those within a circle measuring 0.62 m in diameter. A bicycle wheel rim was used to define this circle, with the target seedling at its center. Target seedling height and stem diameter at ground level were measured as described above, and the following additional data were recorded:

- 1) Distance to the nearest *P. contorta* neighbor.
- 2) Identity of and distance to the nearest interspecific neighbor.
- 3) Numbers and identities of all other plants within the circle.
- 4) Total number of *P. contorta* seedlings within the circle.
- 5) Total number of all vascular plants within the circle.

In all instances, plants that were dead, dying, or much smaller than the target seedling were assumed to represent little competitive threat and were excluded from the analyses.

Simple linear regression was used to examine the relationships between target seedling height or diameter vs:

- 1) total number of vascular plants,
- 2) total number of *P. contorta* seedlings,
- 3) Total number of potential interspecific competitors,
- 4) Distance to the nearest *P. contorta* neighbor, and
- 5) Distance to the nearest interspecific neighbor.

Two sample, independent *t*-tests were used to examine differences between

burn categories for each of these five categories.

Manipulations of the Competitive Environment

At the beginning of the growing season in 1991 (late May, early June) we set up field experiments at Sites 7, 8 and 11 in which the competitive environment of target *P. contorta* seedlings was manipulated (Ellis 1993). At each site, 10 blocks with similar *P. contorta* seedling densities were selected within an area of moderate burn severity. In each block, four 1-m² plots were subjectively selected and permanently marked. The total number of *P. contorta* seedlings was recorded for each plot. Four target seedlings per plot were chosen by dividing the plot into quarters and then selecting a seedling near the center of each quarter. We then randomly assigned one of the following treatments to each plot within a block:

- 1) Removal of all intraspecific and interspecific competitors.
- 2) Removal of all intraspecific competitors.
- 3) Removal of all interspecific competitors.
- 4) No removal of competitors (control).

Therefore, each of the three sites contained 10 replicates of the four treatments. Mean values of the four target seedlings in each plot were used for statistical analyses of treatment effects (i.e. the plot was the sample unit). Potential competitors were clipped at ground level and removed from the appropriate plots. Plots were maintained by clipping any resprouting or colonizing vegetation every 2 weeks in 1991 and periodically in subsequent years. Target seedling performance was tracked over the course of the 1991, 1992, 1993, and 1994 growing seasons by measuring seedling height and stem diameter, as described earlier. Measurements were recorded at the time of plot establishment (week 0) and then at weeks 4, 7, 9, and 14 in 1991. Seedling measurements in 1992, 1993, and 1994 were recorded early (May or

June) in and near the end of the growing season (September).

The results were analyzed with two-way, repeated-measures ANOVA's, with treatment and date as factors. For each of the four treatments, the mean height or diameter of all four target seedlings was taken as the value for any given block, and the mean of all 10 blocks was taken as the site value at each measurement date. Thus, measures were repeated on blocks.

Student-Newman-Keuls multiple range tests, based on the repeated-measures ANOVA, was used to test for significant differences among treatment means.

Competitive Neighborhood Study

The data from 1991 and 1992 showed highly significant increases in growth of target seedlings in response to removal of intraspecific competitors at all three study sites. Given the strength of that response, it seemed likely that differences in target seedling size within the control or interspecific competitors removed plots would reflect the number and size of conspecific competitors. We surmised that a quantitative measure of the competitive environment of target seedlings might enable us to estimate the proportion of variation in seedling size that could be accounted for by variation in competitive environment. Thus, we sought a better measure of the competitive environment of each target seedling.

The proximity of a plant to its neighbors can be examined by the use of Thiessen polygons (e.g., Mead 1966, Liddle et al. 1982, Mithen et al. 1984, Kenkel et al. 1989). Thiessen polygons typically are constructed from a map where plant locations are represented by points (Mithen et al. 1984). Lines are drawn between a target point and all nearby points. Polygons are formed by the intersections of perpendicular bisectors of these lines. The polygon around a particular plant includes all points in the plane that are closer to the plant than to any other, thereby providing an index of the resource area

available to that plant. The polygon also defines the immediate neighbors of a target individual. Thiessen polygons have proven to be useful for assessing competitive effects among even-aged conspecifics (Mithen et al. 1984, Kenkel et al. 1984).

Thiessen polygons were constructed for all target *P. contorta* seedlings in the control and interspecific competitors removed plots at the three study sites. Distance and azimuth were measured from each target seedling to all of its potential competitors. We used the IDRISI geographic information system software (Eastman 1992) to calculate the polygon areas. Regression analyses were used to investigate potential relationships between polygon area and seedling size.

Size of neighbors is likely as important as proximity, so we estimated aboveground biomass of target seedlings and their immediate intraspecific neighbors by double sampling. Height and basal diameter were measured on 30 representative lodgepole seedlings that were growing in the vicinity of each of the three competition sites. The seedlings were then harvested and brought back to the lab, where they were oven dried at 75 for 24 hours. Dry weights of stems and needles were recorded. Regression equations were used to predict biomass of target and neighbor seedlings from measures of height and basal diameter.

To quantify the interspecific neighborhoods of target seedlings we measured cover of all competitors within a 0.25-m radius of target seedlings. Cover should provide a reasonable estimate of the importance of herbaceous or shrub competitors. Cover data were recorded from only those plots in which the intraspecific competitors had been removed. Cover was estimated using a point frame with superimposed crosshairs in a 3 cm grid (Floyd and Anderson 1982). Each cover category was converted to a percentage value by dividing

total intercepts in that category by total intercepts for that study site.

Correlation analyses were used to explore relationships between size of target seedlings and cover of potential interspecific competitors.

RESULTS

Seedling Growth in Moderate and Canopy Burn Plots

Pinus contorta seedlings measured in 1990 were significantly taller, on average, in the canopy burn plots at five of the six sites (Figure 7).

Similarly, mean seedling stem diameter was significantly larger in canopy burn plots than in moderate burn plots at four of the six sites sampled (Figure 7). Mean above-ground biomass on canopy burn plots was 2.9, 1.9, and 3 times higher than that on moderate burn plots at Sites 7, 8, and 11, respectively (Figure 7).

Samples taken at five sites in 1992 confirmed that height and stem diameters of seedlings were greater on canopy burn plots than on moderate burn plots (Table 8). Moreover, there was more variability in both seedling height and diameter on the canopy burn plot than on the paired moderate burn plot at every site (Table 8). This trend is clearly apparent in frequency polygons of seedling height and diameter for moderate and canopy burn plots (Figure 8). These data indicate that not only are seedlings larger, but also that there tends to be relatively more seedlings in the larger size classes on the canopy burn plots.

At all three sites where seedlings were harvested in 1990, seedlings generally accumulated more above-ground biomass per unit height in the severe burn plots than in the moderate burn plots (Figures 9 - 11). This indicates that seedlings in the canopy burn plots were more stocky. The difference was particularly conspicuous and seedlings were considerably larger at Sites 7 and 11 (Figures 9, 11). There was no difference between moderate and canopy burn

plots in the slope of the relationship between aboveground biomass and stem cross-sectional area at any of the three sites ($P > 0.2$ in each case; Figures 9 - 11). Thus, within a site, the amount of stem and leaf biomass supported per unit cross-sectional area of stem was the same for moderate and canopy burn plots.

Seedling Growth in Relation to Site Factors

Across sites, there were significant differences in seedling height, seedling stem diameter, and biomass in both canopy and moderate burn plots (Figure 7). Mean above-ground biomass in the canopy burn plot at Site 7 was 3.1 and 1.7 times that at Sites 8 and 11, respectively (Figure 7). At Site 11, the slope of the relationship between above-ground biomass and stem cross-sectional area was significantly ($P < 0.001$) higher than that at Sites 7 and 8 (cf. Figures 9, 10, and 11), indicating that seedlings at Site 11 were able to support more above-ground biomass per unit cross-sectional area of stem.

Competitive Environment in Moderate and Canopy Burn Plots

The mean number of potential competitors within 0.31 m of a target *Pinus contorta* seedling was significantly greater in the moderate burn than in the canopy burn plot at all five sites sampled (Table 9). The mean number of potential intraspecific competitors was higher in the moderate burn plot at four of the five sites, and the mean number of interspecific competitors also was higher at four of the five sites in the moderate burn plot (Table 9). Mean distance from a target seedling to the nearest intraspecific competitor was greater in the canopy burn plot at three of the five sites, and the difference was marginally significant at the other two sites ($P = 0.06$ and 0.09 at Sites 10 and 12, respectively; Table 9). In contrast, distance to the nearest interspecific competitor was significantly greater in the canopy

burn plot at only two of the five sites (Table 9).

Correlation analyses of *Pinus contorta* seedling heights or diameters vs. numbers, types, or distances of potential competitors revealed few significant relationships, and the results were inconsistent. Significant correlations occurred only for three of the five sites (Table 9). At Site 7, seedling height and diameter were negatively correlated with mean number of all competitors in the moderate burn plot (Table 9). Similarly, at Site 10, seedling diameter was negatively correlated with mean number of all competitors. At both sites, interspecific competitors appeared to exert the strongest influence (Table 9). In contrast, at Site 12, seedling height and diameter were positively correlated with numbers of interspecific or all competitors in the moderate burn plot, whereas in the canopy burn plot, those correlations were negative (Table 9).

Effects of Removal of Competitors on Seedling Growth

Removal of intraspecific competitors resulted in significant increases in height and stem diameter of target *Pinus contorta* seedlings at all three study sites (Figures 12 - 14; Tables 10 - 12). Removing interspecific competitors had minor effects on seedling growth. At Sites 8 and 11, and for stem diameter at Site 7, seedling growth on plots where interspecific competitors were removed was not statistically different from that of controls (Tables 10 - 12). With the exception of stem diameter at Site 11 (Figure 14; Table 12b), the effects of removing all potential competitors and of removing only intraspecific competitors were statistically indistinguishable. Only for Site 7 do the data suggest a significant effect of interspecific competitors; in this case, seedlings became significantly taller in all removal treatments than in the controls (Figure 12; Table 10a).

Mean density of *Pinus contorta* seedlings on the manipulation plots prior

to removal of intraspecific competitors ranged from 36 m^{-2} at Site 7 to 134 m^{-2} at Site 11 (Table 13). Cover of potential interspecific competitors ranged from 23% at Site 7 to 33% at Site 11 (Table 13). Thus, abundance of all potential competitors was highest at Site 11 and lowest at Site 7. The composition of the suite of interspecific competitors was similar at Sites 8 and 11, where *Carex rossii* and *Epilobium angustifolium* were the most abundant species (Table 13). In contrast, *Arnica cordifolia*, *Taraxacum officinale*, and perennial grasses were more important at Site 7.

Seedlings grew more rapidly at Site 7, both with and without the presence of competitors (Figures 12 - 14). This is consistent with the data in Figure 7, where it is shown that above-ground biomass of seedlings harvested in 1991 from moderate and canopy burn plots was higher for seedlings at Site 7 than at Sites 8 or 11. That these site differences were apparent when competitors were removed provides additional evidence that the growing conditions were generally more favorable at Site 7. However, the relative effects of removing competitors were generally consistent with the expectation that competitive effects would be density dependent. Seedling height after four years was 21%, 39%, and 34% greater and stem diameters were 48%, 66%, and 89% greater with all competitors removed at Sites 7, 8, and 11, respectively. Thus, the magnitude of competitive effects was roughly proportional to the density of intraspecific competitors.

At Site 7, target seedling height on plots with all conspecific competitors removed was negatively correlated with cover of potential interspecific competitors (Table 14). At Site 8 on the same treatment plots, both height and stem diameter of target seedlings were negatively correlated with cover of interspecific competitors (Table 14). At Site 11, neither height nor stem diameter were correlated with interspecific competitor cover.

Pinus contorta seedling height and stem diameter were positively correlated with "available area" as estimated by Thiessen polygons at Site 8 but not at Sites 7 or 11 (Table 15; Figure 15). The range of seedling sizes and polygon areas was similar for the three sites (data not shown); thus the differences among sites did not appear to be a consequence of limited variability in polygon area at Sites 7 or 11.

Seedling above-ground biomass was closely correlated with both seedling height and stem diameter ($r > 0.86$ in all cases), so we used the summation of either heights or stem diameters of neighboring seedlings (those defining the Thiessen polygons) as surrogates for the size of potential conspecific competitors. Contrary to expectations, we found no evidence that size of target seedlings on plots having intraspecific competitors was negatively correlated with the size of potential competitors (Table 16). In fact, the only significant correlations were positive (e.g. Figure 15), indicating, in those cases, that individual seedlings tended to occur in neighborhoods of similar sized seedlings.

DISCUSSION

Effects of Fire Severity on Growth of *Pinus contorta* Seedlings

Samples taken in 1990 and 1990 demonstrate that *Pinus contorta* seedlings consistently grew faster in areas subjected to severe crown fires than in adjacent areas subjected to fire of moderate severity (Figures 7, 8; Table 8). In addition, seedlings in the canopy burn areas were generally more robust, supporting more above-ground biomass per unit height. These differences in seedling growth could reflect differences in abiotic conditions or differences in the competitive environment between moderate and canopy burn areas, or both. Data from the plots where we manipulated the competitive environment of target *Pinus contorta* seedlings (Figures 12, 13, 14) show

clearly that intraspecific competition can affect seedling growth. Thus, faster growth in the canopy burn areas may, in part, reflect lower densities of seedlings. However, the fact that we did not find consistent relationships between seedling size and various indices of the immediate competitive environment (Tables 9, 14, 15) suggests that differences in abiotic factors may be largely responsible for the observed size differences between moderate and canopy burn areas. We think it unlikely that there were substantial postfire differences in soil nutrient availability between the adjacent plots (although, as discussed below, we suspect that fine-scale heterogeneity may be very important within plots). The moderate burn areas were subjected to intense surface fires that consumed most of the litter and duff on the forest floor, so that nutrient inputs from accumulated organic matter likely were comparable in the two fire severity classes. Ash from the consumption of needles and fine twigs in the canopy burn areas may have deposited additional nutrients, but one would also expect higher losses due to volatilization in those areas. It seems more likely that the observed difference in seedling size was due to light availability. Quantifying irradiance or temperature regimes in moderate and canopy burn plots was beyond the scope of this study, but casual observations indicated that considerably more light reached the forest floor in canopy burn plots. This was a simple consequence of the fact that needles, fine twigs and branches, and many cones were consumed in crown fires, resulting in a much more open postfire canopy. Thus, more light would have been available for photosynthesis, and temperatures probably would have been more favorable for metabolic processes in the canopy burn plots. Furthermore, it is likely that snow would melt earlier in crown fire areas and that temperatures would become favorable for growth earlier in the season.

Seedling Growth in Relation to Site Factors

Our studies of factors affecting seedling growth were restricted to the six low and mid elevation sites that had the highest seedling densities (Sites 7 - 12; Figure 2) in an effort to determine whether seedling growth was dependent upon seedling density. Neither seedling height nor stem diameter was correlated with seedling density across the six sites on either moderate or canopy burn plots; in fact, Site 11, which had by far the highest seedling densities, had the second tallest seedlings and, on canopy burn plots, seedlings with the second largest stem diameters (Figure 7). There can be little doubt, based on the results from our competitor manipulation experiments, that intraspecific competition affects seedling growth over the range of densities represented by the moderate burn plots at these sites (Figures 12 - 14), but those density-dependent effects clearly are secondary to environmental differences among the sites, such as nutrient and water availability, soil depth and moisture storage capacity, and temperature.

Site 7, which consistently produced the largest seedlings of any site in the study (Figures 7, 12), appeared to be the most mesic, supporting numerous mature *Picea engelmannii* trees in the prefire stand. Although the underlying substrate at Site 7 is basalt, the soils appear to be derived from glacial till as evidenced by the presence of large and small rounded boulders. Furthermore, the site has a southeasterly aspect. Similarly, Site 11, which supports a vigorous growth of understory forbs and perennial grasses (Table 13), is among the more mesic of the low and mid elevation sites. In contrast, the soils at Site 8, which produced relatively small seedlings (Figures 7, 13), were derived from rhyolite, which typically produces coarse textured, infertile soils (Despain 1990). This site has a southwesterly aspect and appears to be among the more xeric of the sites. These results are not surprising; differences in site index among areas supporting stands *Pinus*

contorta are well known (e.g., see Alexander and Edminster 1980).

Effects of Interspecific vs. Intraspecific Competition on Growth of *Pinus contorta* Seedlings

Removing intraspecific competitors consistently had a far greater effect on growth of target *Pinus contorta* seedlings than did removal of interspecific competitors (Figures 12 - 14). In fact, effects of removing interspecific competitors were slight and only statistically detectable in two cases: height growth at Site 7 (Table 10a) and stem diameter growth at Site 11 (Table 12b). In the absence of conspecific competitors, negative relationships between interspecific competitor cover and size of target seedlings were found at two of three sites (Table 14), but these effects would have been minor compared to those of intraspecific competitors in the natural competitive environment. We anticipated that the intraspecific competition would have stronger effects on seedling growth, but the scarcity of perceptible effects of interspecific competitors was unexpected given the emphasis on the importance of interspecific competitors by other investigators (e.g. Brown 1975, Lotan and Perry 1983, Lotan et al. 1985, Powell et al. 1994). The significant, if modest, effects of interspecific removals at Site 7 (Table 10a) and Site 11 (Table 12b) are likely attributable to the presence of *Calamagrostis rubescens*, a strongly rhizomatous, robust perennial that is thought to be among the most important interspecific competitors with *Pinus contorta* seedlings (Lotan and Perry 1983). *C. rubescens* was common at both sites, and given its vigorous growth and height, may have reduced soil resources as well as light availability to neighboring *Pinus contorta* seedlings. In a companion study of microhabitat characteristics affecting seedling growth (von Dohlen et al., manuscript), we observed that one and two year old *Pinus contorta* seedlings growing in or near *C. rubescens* were

typically spindly with few needles. At Site 8, the most abundant interspecific competitor was *Carex rossii* (Table 13). These short-statured sedges apparently had little influence on growth of *Pinus contorta* seedlings.

Our data (Part 1, Anderson and Romme 1991) show that the abundance of potential competitors had little or no influence on the postfire establishment of *Pinus contorta* over a broad range of sites in Yellowstone National Park. Lyon's (1984) results indicated that interspecific competitors had little effect on survival of *Pinus contorta* seedlings following the Sleeping Child Fire in Montana. Given the minor effects of interspecific competitors on growth of *Pinus contorta* seedlings documented here, it seems reasonable to conclude that interspecific competitors play a minor role in the recovery of *Pinus contorta* following stand-replacing fires. Interspecific competitors may have much more significant effects in forest clear-cuts, especially if aggressive aliens are seeded into the sites (Powell et al. 1994).

Effects of Microscale Heterogeneity on Growth of Pinus contorta Seedlings

If environmental conditions were homogeneous with respect to availabilities of light, water, and nutrients, differences in seedling performance would reflect genetic variation in growth potential and differences in the competitive environment among individuals. That we did not find close correlations between size of seedlings and various parameters thought to index the intensity of competition (Tables 9a, 9b, 14, 15) suggests that micro-scale environmental heterogeneity may be a critical factor affecting early seedling growth. Of course, we don't know the extent to which individual seedlings may vary in genetic potential for rapid growth, but the fact that size of target seedlings was, in some cases, positively correlated with the size of their closest intraspecific neighbors (Table 16) indicates that local differences in environmental conditions, such as soil fertility or

shading by standing dead trees, may be very important. We cannot, however, rule out the possibility, that many seedlings in a local neighborhood may be at least half-siblings with similar genetic potentials.

Other studies also have found that neighbors of large plants tend to be large, and vice versa (Reed and Burkhart 1985, Kenkel et al. 1989), but such autocorrelations are thought to result from self-thinning in response to competition for light which selectively removes smaller trees and leaves the relatively larger trees in a local patch. This results in a positive autocorrelation because the only small trees that survive the self-thinning are those surrounded by other small trees (Kenkel et al. 1989). It is clear, however, that competition for light and self-thinning cannot explain the positive correlation between size of target seedlings and their neighbors in this study. Exposure of local groups of seedlings to similar environmental conditions in a heterogeneous environmental matrix appears to be the most plausible explanation.

Studies that have addressed the importance of local crowding on growth typically have found that the local competitive environment accounts for only a relatively small fraction of observed variability in size (e.g., Mead 1966, Mack and Harper 1977, Watkinson et al. 1983, Mithen et al. 1984, Eissenstat and Caldwell 1988). Eissenstat and Caldwell (1989) caution that "easily measured attributes of neighboring plants such as shoot size and proximity may not relate to the intensity of root interactions."

Of the various indices of local crowding, available area, as estimated by Thiessen polygons, has most frequently been found to correlate with plant growth (Mead, 1966, Liddle et al. 1982, Mithen et al. 1984, Matlack and Harper 1986, Kenkel et al. 1989). We found that seedling size was positively correlated with available area at only one of three study sites (Table 15).

At that site, however, the relationship was highly significant (Figure 15). It is not immediately clear why a strong relationship was found at Site 8 but not at Sites 7 and 11. Seedling densities at Site 8 were intermediate in relation to the other two sites, making it unlikely that the differences in responses were related to seedling densities. Another possibility is that area is somehow more critically related to available resources at Site 8. As noted earlier, seedlings were smaller at Site 8 than at Sites 7 or 11, and our general impression is that Site 8 is more xeric (and probably less fertile) as a consequence of coarse-textured soils derived from rhyolite. The soils at that site may be shallower and have lower water holding capacities. Thus, available area may be a relatively more important parameter affecting seedling growth at Site 8 because soil resources tend to be more limiting.

Conclusions

A major objective of this portion of our research was to identify the factors that determine which *Pinus contorta* seedlings might become eventual dominants in postfire stands. We anticipated that competition from conspecific as well as interspecific neighbors would have a major influence on the growth of individual seedlings. We have demonstrated that competition among seedlings can be intense and that removal of intraspecific neighbors will result in substantial gains in size of the remaining target seedlings. However, our data suggest that competitive effects are secondary to the effects of fine-scale heterogeneity in resource availability and, perhaps, to genetic variability among seedlings. Which seedlings become stand dominants is not simply a consequence of available area or proximity and size of neighbors. Instead, it appears that numerous factors interact to determine the fate of individual seedlings. Several of these factors are probably stochastic (e.g., the proximity of a seedling to standing dead trees that may

cast shade on it for several hours each day). If differential seedling performance and, ultimately, survivorship is largely a consequence of local environmental conditions and, at least to some extent, the local competitive environment, both of which probably are highly stochastic, selection for genetically "superior" individuals may be precluded (Kenkel et al. 1989). A seed that lands and germinates in a fertile microsite and that happens to have few neighbors may become a stand dominant and survive to contribute progeny to the next generation regardless of its genetic potential. On the other hand, a "superior" seedling may become established on an impoverished microsite or in a highly competitive neighborhood only to have its fate sealed by being overtapped. Thus, chance may serve to maintain the genetic diversity within the population (Kenkel et al. 1989).

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Table 1. Characteristics of study sites in Yellowstone National Park, Wyoming. Substrate indicates parent material as shown by USGS (1972). Habitat type follows Steele et al. (1983). Stage refers to the cycle of *P. contorta* stand development as described by Romme and Despain (1989). Where two stages are shown, the stand was intermediate but tended toward the first stage listed. Serotiny is the proportion of trees in the stand having serotinous cones.

	Site	Elev (m)	Substrate	Habitat type	Stage	Serotiny (%)

1	Solfatara Plateau	2490	rhyolite	ABLA/VASC	LP 3/2	0
2	Mt. Washburn	2560	andesite	ABLA/VASC	LP 4	11
3	Lewis River	2500	rhyolite	ABLA/VASC	LP 2/3	0
4	Lewis Lake	2350	rhyolite	ABLA/VASC	LP 2/3	0
5	Norris Jct. East	2270	alluvium	ABLA/CARU	LP 2	0
6	Indian Creek	2260	basalt	PICO/VASC	LP 2	48
7	Swan Lake Flat	2270	basalt	PIEN/ARCO	LP 2	13
8	Whiskey Flat	2290	rhyolite	PICO/VASC	LP 1/2	48
9	Norris Jct. South	2320	rhyolite	PICO/VASC	LP 2	4
10	West Yellowstone	2040	alluvium	PICO/PUTR	LP 2	15
11	Madison River Bridge	2100	tuff	PICO/CARU	LP 1	45
12	Madison Junction	2120	rhyolite	PICO/CARO	LP 1	44

Table 2. Mean stand age at time of fire, prefire stand density, postfire density of *P. contorta* seedlings and cones on the ground, and mean postfire number of cones remaining in crown of burned *P. contorta* trees for each of the study plots at 12 study sites in Yellowstone National Park. Data were taken in 1990 from *P. contorta* forests that burned in 1988 (see Table 1). Burn severity classes are described in Methods; R. Canopy = remote severe canopy burn. NA indicates that there was no remote canopy burn plot at that site.

Plot	Study Site											
	1	2	3	4	5	6	7	8	9	10	11	12
Mean Stand Age (years)												
Unburned	243	204	163	165	116	197	138	99	116	67	111	109
Moderate	165	195	171	187	119	205	131	96	111	118	108	96
Canopy	131	196	163	170	116	191	129	99	111	115	103	98
R. Canopy	127	176	153	137	NA	178	125	101	113	NA	110	103
Prefire Stand Density (trees/ha)												
Unburned	1390	1180	728	880	1250	666	710	4920	1620	1546	3133	9400
Moderate	780	1400	1160	1090	990	1490	970	5160	2140	2360	4580	16900
Canopy	1440	1390	2400	1170	1140	1380	990	4880	2300	1230	3120	12480
R. Canopy	1390	1240	1590	980	NA	1740	1050	4660	2410	NA	2580	8880
Postfire Seedling Density (seedlings/ha)												
Moderate	5600	13200	38600	76800	45000	83800	216300	164600	98600	83200	1906000	663600
Canopy	870	3300	1640	7800	6800	12200	37800	26600	9400	21200	226400	145600
R. Canopy	80	1900	440	3800	NA	6000	9400	29000	5400	NA	363600	80400
Postfire Cones on Ground Cones (cones/m ²)												
Moderate	2.98	3.4	6.86	9.88	3.92	10.84	6.23	4.24	5.34	8.72	30.2	10.74
Canopy	0.11	0.95	0.028	0.38	0.52	7.28	1.28	0.98	0.4	0.5	6.12	2.28
R. canopy	0.12	0.21	0.24	0.06	NA	1.68	0.68	1.34	0.86	NA	8.14	2.5
Postfire Cones in Canopy (cones/tree)												
Moderate	83	152*	342*	553*	161	409	346	246	258	299	424	171*
Canopy	48	58	24	82	200	267	228	167	251	240	315	63

*Indicates significant difference ($P < 0.05$) between moderate burn and canopy burn plots.

Table 3. Ratios of postfire seedling to prefire stand densities in moderate burn, canopy burn, and remote canopy burn plots at 12 study sites in Yellowstone National Park. NA = No remote canopy plot at that site.

* = Transects with insufficient seedlings to replace the prefire stand.

Site	Location	Moderate	Canopy	Remote Canopy
1	Solfatara Plateau	7.7	0.4*	0.1*
2	Mt. Washburn	9.3	2.4	1.1
3	Lewis River	33.6	0.7*	0.3*
4	Lewis Lake	65.8	7.2	3.3
5	Norris Jct. East	45.4	5.9	NA
6	Indian Creek	56.7	8.7	3.4
7	Swan Lake Flat	214.0	37.4	9.5
8	Whiskey Flat	31.9	5.1	6.2
9	Norris Jct. South	45.8	4.1	2.2
10	W. Yellowstone	35.2	17.1	NA
11	Madison River Bridge	402.0	76.3	141.0
12	Madison Junction	38.8	13.4	9.3

Table 4. Comparison of the proportion of serotinous trees in the permanent unburned plot at nine study sites in Yellowstone National Park with that of another unburned stand (or stands) in the general vicinity.

Site	Incidence of Serotiny (%)		Distance/Direction from Permanent Plot
	Permanent Plot	Additional Plot(s)	
1	0	0	Within 3 km in all directions
3	0	0	Within 1 km in all directions
4	0	0	Within 1 km in all directions
5	0	14	Within 1 km west
6	48	17	Within 1 km north
7	13	9	Within 1 km south
8	48	42	Within 1 km north and south
9	4	28	Within 1 km east
10	15	64	Within 1 km west

Table 5. Percent cover of all plant and non-plant entities at moderate and canopy burn plots at 12 study sites in Yellowstone National Park during 1990.

Moderate Burn Plots:

Entity	Site											
	1	2	3	4	5	6	7	8	9	10	11	12
Rock	0.2	0.2	0.1	0.0	0.0	0.8	0.0	3.8	3.7	0.0	0.0	0.0
Mineral Soil	8.2	4.6	15.1	2.2	0.8	10.6	24.3	7.8	10.2	7.7	0.0	0.1
Litter	39.9	78.4	63.1	55.2	63.6	43.3	39.8	65.7	67.2	12.9	45.4	49.4
Duff	0.3	0.1	0.0	0.2	0.3	0.0	5.0	3.2	0.2	1.2	0.0	0.0
Burned Litter/Duff	24.3	0.2	5.5	20.6	11.8	0.0	1.1	6.3	3.7	36.7	13.2	3.3
Charcoal	4.5	2.1	3.9	1.0	1.1	0.2	2.9	1.4	1.9	1.9	0.7	0.9
Unburned > 0.25" dia.	1.0	2.8	3.5	1.4	1.2	2.8	3.0	0.3	0.9	0.4	3.8	3.9
Moss/Lichen	5.2	2.5	0.7	1.3	0.3	0.0	4.9	5.1	0.7	0.5	1.1	1.1
Burned 0.25" dia.	7.2	6.4	5.2	4.5	0.3	8.4	2.8	3.3	5.6	4.6	3.1	1.6
Lodgepole seedlings	0.0	0.0	0.3	0.5	1.1	0.3	3.1	1.4	2.0	2.0	11.4	5.9
Other vegetation	9.2	2.6	2.6	12.9	19.6	33.5	17.3	1.8	3.9	31.4	21.2	33.6

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Canopy Burn Plots:

Entity	Site											
	1	2	3	4	5	6	7	8	9	10	11	12
Rock	1.7	0.8	0.9	0.0	0.0	0.9	0.8	2.6	2.4	0.0	1.9	0.9
Mineral Soil	11.6	54.7	71.2	3.8	1.7	77.3	76.7	17.5	18.1	11.1	37.5	20.5
Litter	1.2	0.0	1.3	0.3	4.5	13.6	3.1	5.8	5.9	0.4	0.0	2.6
Duff	0.0	0.0	0.0	0.0	5.4	0.8	0.0	0.4	0.0	0.0	0.0	0.0
Burned Litter/Duff	64.7	16.7	18.2	86.9	74.9	1.1	0.0	48.9	59.4	60.2	29.6	49.1
Charcoal	16.3	11.8	3.4	3.7	7.7	1.1	12.6	11.1	3.8	4.3	8.0	2.3
Unburned > 0.25" dia.	0.0	1.6	0.0	0.1	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Moss/Lichen	0.0	5.6	0.2	1.0	0.0	0.0	0.5	9.6	0.1	0.2	1.0	0.9
Burned 0.25" dia.	4.1	6.3	3.9	3.7	1.3	3.5	0.2	2.4	7.0	6.8	3.6	0.3
Lodgepole seedlings	0.0	0.0	0.0	0.1	0.3	0.2	1.8	0.4	0.1	1.1	4.7	3.8
Other vegetation	0.2	2.6	1.0	0.4	4.1	1.4	4.0	1.3	3.1	15.8	13.7	18.7

Table 6. Annual rate of change in density of *P. contorta* seedlings in moderate, canopy, and remote canopy burn plots at the 12 study sites. Rates were estimated as the slope of a regression of the natural logarithm of the total number of seedlings vs. year, based on data from 1990 - 1994 (see Methods). Positive values indicate net recruitment.

Site	Rate of Density Change (%)		
	Moderate	Canopy	Remote
1 Solfatara Plateau	-3.9	0	+35.0
2 Mt. Washburn	-40.8	-9.2	-26.0
3 Lewis River	-5.8	+3.8	0
4 Lewis Lake	-10.2	-4.0	-8.6
5 Norris Jct. East	+7.8	0	
6 Indian Creek	-13.0	-4.0	0
7 Swan Lake Flat	-2.6	-3.8	-5.4
8 Whiskey Flat	0	0	-2.2
9 Norris Jct. South	-0.8	-3.2	-2.9
10 W. Yellowstone	-2.8	0	
11 Madison River Bridge	-4.4	-1.9	-2.4
12 Madison Junction	-2.7	-2.0	0

Table 7. (A) Annual rate of change in density of *P. contorta* seedlings in control and interspecific competitors removed (ICR) plots from 1991 to 1993 at three study areas. The plots were all in areas of moderate burn severity (see Methods, Part 2, for details). Rate of change was estimated as the slope of the change in the natural logarithm of seedling totals over the 2 years.

Study Site	Treatment	Seedling Density (m ⁻²)		Rate of Density Change (%)
		1991	1993	
Madison River Bridge	ICR	135	127	-2.7
	Control	151	141	-3.4
Swan Lake Flat	ICR	27	26	0
	Control	29	27	-4.3
Whiskey Flat	ICR	80	79	-0.8
	Control	80	83	0

(B) Annual mortality rates for marked target seedlings in control and ICR plots (pooled) from 1991 to 1994. Four seedlings were marked in each of ten quadrats for both treatments at each area (4 X 10 X 2 = 40). Mortality rates were estimated as the change in the natural logarithm of seedling totals over the 3 years. Total seedling densities for these plots are given in (A).

Study Site	Treatment	Seedling 1991	Totals 1994	Mortality Rate (%)
Madison River Bridge	ICR	40	39	
	Control	40	38	
	Total	80	77	1.3
Swan Lake Flat	ICR	40	39	
	Control	40	39	
	Total	80	78	0.8
Whiskey Flat	ICR	40	38	
	Control	40	38	
	Total	80	76	1.7

Table 8a. Results of a two-sample *t*-tests for differences in mean stem diameters of *Pinus contorta* seedlings in moderate and canopy burn areas at five sites in Yellowstone National Park in June, 1992.

Site	Burn Type	N	Diameter (mm)	S.D.	t	P
11	Moderate	200	1.84	0.93	-14.84	<0.001
	Canopy	200	3.64	1.44		
12	Moderate	200	2.01	0.08	-13.66	<0.001
	Canopy	200	3.59	1.42		
9a	Moderate	200	2.67	1.21	-10.17	<0.001
	Canopy	200	4.74	2.62		
9b	Moderate	200	1.38	0.64	-15.58	<0.001
	Canopy	200	3.20	1.50		
7	Moderate	200	4.16	1.70	-10.64	<0.001
	Canopy	200	6.59	2.74		
10	Moderate	200	4.35	1.73	-4.28	<0.001
	Canopy	200	5.28	2.53		

Table 8b. Results of a two-sample *t*-test for mean height of *Pinus contorta* seedlings in moderate and canopy burn areas at five sites in Yellowstone National Park in June, 1992.

Site	Burn Type	N	Height (cm)	S.D.	t	P
11	Moderate	200	12.59	5.59	-12.09	<0.001
	Canopy	200	19.82	6.34		
12	Moderate	200	13.91	5.15	-7.46	<0.001
	Canopy	200	18.40	6.78		
9a	Moderate	200	13.13	6.16	-7.80	<0.001
	Canopy	200	18.76	7.85		
9b	Moderate	200	6.90	3.20	-15.11	<0.001
	Canopy	200	14.52	6.39		
7	Moderate	200	20.67	8.40	-6.51	<0.001
	Canopy	200	26.70	10.05		
10	Moderate	200	20.89	7.31	-10.64	<0.001
	Canopy	200	24.84	9.39		

Table 9a. Mean numbers of intraspecific, interspecific, and total competitors within a 0.31 m radius of target seedlings, and mean distances from target seedlings to the nearest intraspecific or interspecific competitor, in moderate and canopy burn plots at five study sites in Yellowstone National Park. P is the probability that the difference between moderate and canopy burn plots is due to chance.

	Number of Competitors			Mean distance (cm) to nearest competitor	
	Intraspecific	interspecific	Total	Intraspecific	interspecific
<u>Site 7</u>					
Moderate	7.0	12.0	17.0	12.0	10.0
Canopy	1.0	9.0	10.0	21.0	13.0
P	0.001	0.05	0.001	0.001	0.095
<u>Site 8</u>					
Moderate	12.0	7.0	19.0	10.0	17.0
Canopy	3.0	1.0	4.0	20.0	26.0
P	0.001	0.02	0.010	0.001	0.001
<u>Site 9</u>					
Moderate	4.0	7.0	11.0	15.0	15.0
Canopy	1.0	3.0	4.0	27.0	19.0
P	0.001	0.05	0.001	0.001	0.116
<u>Site 10</u>					
Moderate	2.0	15.0	18.0	21.0	14.0
Canopy	1.0	3.0	4.0	26.0	23.0
P	0.119	0.001	0.001	0.06	0.001
<u>Site 12</u>					
Moderate	16.0	35.0	51.0	10.0	6.0
Canopy	5.0	25.0	30.0	13.0	8.0
P	0.001	0.188	0.077	0.09	0.198

Table 9b. Results of correlation analyses between height and diameter of target *Pinus contorta* seedlings vs. density of intraspecific, interspecific, or all competitors, or vs. distance to the nearest intraspecific or interspecific competitor in moderate burn can canopy burn plots at three study sites in Yellowstone National Park. NS = no significant correlation.

		Site 7		Moderate		Canopy	
		r	P	r	P	r	P
Height	Intraspecific competitors	NS	NS	NS	NS	NS	NS
	Interspecific competitors	NS	NS	NS	NS	NS	NS
	All competitors	-0.390	0.049	NS	NS	NS	NS
	Nearest intraspecific competitor	NS	NS	NS	NS	NS	NS
	Nearest interspecific competitor	NS	NS	NS	NS	NS	NS
Diameter	Intraspecific competitors	NS	NS	NS	NS	NS	NS
	Interspecific competitors	-0.530	0.060	NS	NS	NS	NS
	All competitors	-0.460	0.020	NS	NS	NS	NS
	Nearest intraspecific competitor	NS	NS	NS	NS	NS	NS
	Nearest interspecific competitor	NS	NS	NS	NS	NS	NS
		Site 10		Moderate		Canopy	
		r	P	r	P	r	P
Diameter	Intraspecific competitors	NS	NS	NS	NS	NS	NS
	Interspecific competitors	-0.450	0.022	NS	NS	NS	NS
	All competitors	-0.470	0.016	NS	NS	NS	NS
	Nearest intraspecific competitor	NS	NS	NS	NS	NS	NS
	Nearest interspecific competitor	NS	NS	NS	NS	NS	NS
		Site 12		Moderate		Canopy	
		r	P	r	P	r	P
Height	Intraspecific competitors	NS	NS	0.410	0.040	0.410	0.040
	Interspecific competitors	0.410	0.040	-0.480	0.014	-0.480	0.014
	All competitors	0.470	0.018	-0.410	0.040	-0.410	0.040
	Nearest intraspecific competitor	-0.540	0.005	NS	NS	NS	NS
	Nearest interspecific competitor	NS	NS	NS	NS	NS	NS
Diameter	Intraspecific competitors	NS	NS	0.41	0.040	0.41	0.040
	Interspecific competitors	0.620	0.001	-0.630	0.001	-0.630	0.001
	All Competitors	0.610	0.001	-0.580	0.020	-0.580	0.020
	Nearest intraspecific competitor	-0.410	0.040	NS	NS	NS	NS
	Nearest interspecific competitor	-0.430	0.030	0.420	0.040	0.420	0.040

Table 10a. Two-way, repeated-measures analysis of variance (ANOVA) of the effects of removal of intraspecific, interspecific, or all competitors on target seedling height over four growing seasons at Site 7 (see Figure 12). Final means for each treatment and results of Student-Newman-Keuls multiple range test (based on repeated-measures ANOVA) are shown below ANOVA table. Treatments connected by the same vertical line did not differ significantly at $P = 0.05$.

Source of					
Variation	DF	SS	MS	F	P
Rep	9.0	3439.18	382.120		
Treatment	3.0	2034.82	678.272	5.89	0.003
Treatment x Rep	27.0	3110.60	115.207		
Date	7.0	81982.00	11712.000	583.73	< 0.001
Date x Rep	63.0	1264.00	20.064		
Treatment x Date					
	21.0	794.06	37.81	5.18	< 0.001
Residual	189.0	1378.84	7.295		
Total	319.0	94003.00	294.681		

Treatment	Mean (cm)	
All competitors removed	70.0	
Intraspecific competitors removed	65.4	
Interspecific competitors removed	63.0	
Control (no competitors removed)	57.9	

Table 10b. Two-way, repeated-measures analysis of variance (ANOVA) of the effects of removal of intraspecific, interspecific, or all competitors on target seedling stem diameter over four growing seasons at Site 7 (see Figure 12). Final means for each treatment and results of Student-Newman-Keuls multiple range test (based on repeated-measures ANOVA) are shown below ANOVA table. Treatments connected by the same vertical line did not differ significantly at $P = 0.05$.

Source of					
Variation	DF	SS	MS	F	P
Rep	9.0	180.50	20.056		
Treatment	3.0	497.41	165.802	16.825	< 0.001
Treatment x Rep	27.0	266.07	9.854		
Date	7.0	5119.40	731.343	626.338	< 0.001
Date x Rep	63.0	73.56	1.168		
Treatment x Date					
	21.0	212.80	10.133	15.348	< 0.001
Residual	189.0	124.78	0.660		
Total	319.0	6474.52	20.296		

Treatment	Mean (mm)	
All competitors removed	19.1	
Intraspecific competitors removed	17.8	
Interspecific competitors removed	13.8	
Control (no competitors removed)	12.8	

Table 11a. Two-way, repeated-measures analysis of variance (ANOVA) of the effects of removal of intraspecific, interspecific, or all competitors on target seedling height over four growing seasons at Site 8 (see Figure 13). Final means for each treatment and results of Student-Newman-Keuls multiple range test (based on repeated-measures ANOVA) are shown below ANOVA table. Treatments connected by the same vertical line did not differ significantly at $P = 0.05$.

Source of Variation	DF	SS	MS	F	P
Rep	9.0	1919.13	213.236		
Treatment	3.0	3511.24	1170.414	14.019	< 0.001
Treatment x Rep	27.0	2254.17	83.488		
Date	7.0	27872.00	3981.679	522.349	< 0.001
Date x Rep	63.0	480.23	7.623		
Treatment x Date					
	21.0	1207.86	57.517	15.449	< 0.001
Residual	189.0	703.63	3.723		
Total	319.0	37948.00	118.959		

Treatment	Mean (cm)
All competitors removed	45.8
Intraspecific competitors removed	47.7
Interspecific competitors removed	35.1
Control (no competitors removed)	33.0

Table 11b. Two-way, repeated-measures analysis of variance (ANOVA) of the effects of removal of intraspecific, interspecific, or all competitors on target seedling stem diameter over four growing seasons at Site 8 (see Figure 13). Final means for each treatment and results of Student-Newman-Keuls multiple range test (based on repeated-measures ANOVA) are shown below ANOVA table. Treatments connected by the same vertical line did not differ significantly at $P = 0.05$.

Source of

Variation	DF	SS	MS	F	P
Rep (Block)	9.0	118.29	13.144		
Treatment	3.0	442.01	147.336	31.153	< 0.001
Treatment x Rep	27.0	127.69	4.729		
Date	7.0	2052.40	293.200	309.867	< 0.001
Date x Rep	63.0	59.61	0.946		
Treatment x Date					
	21.0	185.54	8.835	22.156	< 0.001
Residual	189.0	75.37	0.399		
Total	319.0	3060.91	9.595		

Treatment	Mean (mm)
All competitors removed	12.4
Intraspecific competitors removed	12.1
Interspecific competitors removed	7.6
Control (no competitors removed)	7.4

Table 12a. Two-way, repeated-measures analysis of variance (ANOVA) of the effects of removal of intraspecific, interspecific, or all competitors on target seedling height over four growing seasons at Site 11 (see Figure 14). Final means for each treatment and results of Student-Newman-Keuls multiple range test (based on repeated-measures ANOVA) are shown below ANOVA table. Treatments connected by the same vertical line did not differ significantly at $P = 0.05$.

Source of Variation	DF	SS	MS	F	P
Rep	9.0	4895.76	543.974		
Treatment	3.0	4077.41	1359.135	15.856	< 0.001
Treatment x Rep	27.0	2314.39	85.718		
Date	7.0	32890.00	4698.632	196.183	< 0.001
Date x Rep	63.0	1508.87	23.950		
Treatment x Date					
	21.0	1272.36	60.589	12.831	< 0.001
Residual	189.0	892.49	4.722		
Total	319.0	47852.00	150.005		

Treatment	Mean (cm)
All competitors removed	50.9
Intraspecific competitors removed	54.0
Interspecific competitors removed	40.0
Control (no competitors removed)	38.1

Table 12b. Two-way, repeated-measures analysis of variance (ANOVA) of the effects of removal of intraspecific, interspecific, or all competitors on target seedling stem diameter over four growing seasons at Site 11 (see Figure 14). Final means for each treatment and results of Student-Newman-Keuls multiple range test (based on repeated-measures ANOVA) are shown below ANOVA table. Treatments connected by the same vertical line did not differ significantly at $P = 0.05$.

Source of Variation	DF	SS	MS	F	P
Rep (Block)	9.0	148.56	16.507		
Treatment	3.0	531.91	177.305	61.841	< 0.001
Treatment x Rep	27.0	77.41	2.867		
Date	7.0	1541.18	220.169	346.302	< 0.001
Date x Rep	63.0	40.05	0.636		
Treatment x Date					
	21.0	200.17	9.532	44.029	< 0.001
Residual	189.0	40.92	0.217		
Total	319.0	2580.20	8.088		

Treatment	Mean (mm)
All competitors removed	11.9
Intraspecific competitors removed	11.0
Interspecific competitors removed	6.9
Control (no competitors removed)	6.3

Table 13. Absolute cover (%) of vascular plants in plots from which intraspecific competitors had been removed at three study sites in Yellowstone National Park. Interspecific cover is cover of potential interspecific competitors with target *Pinus contorta* seedlings. Mean densities of *P. contorta* seedlings (m^{-2}) in the experimental plots prior to density manipulations is also shown. See Methods for experimental details.

SPECIES	SITE		
	7	8	11
<i>Achillea millefolium</i>	0.29	—	—
<i>Agoseris glauca</i>	0.17	—	—
<i>Anaphalis margaritacea</i>	—	—	0.35
<i>Antennaria racemosa</i>	—	0.56	—
<i>Arnica cordifolia</i>	7.42	0.17	—
<i>Calamagrostis canadensis</i>	0.03	0.28	—
<i>Calamagrostis rubescens</i>	—	—	4.27
<i>Carex rossii</i>	0.11	19.84	12.99
<i>Ceanothus velutinus</i>	—	—	0.05
<i>Collinsia parviflora</i>	—	—	0.11
<i>Epilobium angustifolium</i>	3.43	3.44	10.78
<i>Epilobium ciliatum</i>	0.35	—	—
<i>Hieracium albiflorum</i>	—	2.11	0.60
<i>Pinus contorta</i>	22.73	16.10	15.35
<i>Populus tremuloides</i>	0.05	0.31	1.01
<i>Ribes</i> spp.	—	0.35	0.89
<i>Salix scouleriana</i>	—	—	0.70
<i>Senecio</i> spp.	0.25	—	—
<i>Solidago</i> spp.	0.29	—	—
<i>Spiraea betulifolia</i>	—	—	0.51
<i>Symporicarpos</i> spp.	—	—	0.01
<i>Taraxacum officinale</i>	5.48	—	0.25
Unknown forb	0.31	—	—
Unknown grasses	5.19	—	—
Total Cover	46.1	43.2	47.9
Interspecific Cover	23.4	27.1	32.5
<i>P. contorta</i> Density (m^{-2})	36	81	134

Table 14. Summary of correlation analyses between height or stem diameter of target *Pinus contorta* seedlings and the cover of potential interspecific vascular plant competitors at three study sites in Yellowstone National Park. These analyses were restricted to target seedlings and cover estimates on treatment plots from which all conspecific competitors had been removed. Treatments were imposed in May of 1991 and interspecific cover was sampled in June of 1993.

	Site 7			Site 8			Site 11		
	r	P	n	r	P	n	r	P	n
Height	-0.35	0.035	37	-0.35	0.026	40	0.24	0.14	40
Diameter	-0.24	0.150	37	-0.34	0.030	40	0.13	0.42	40

Table 15. Summary of correlation analyses between height or stem diameter of target *Pinus contorta* seedlings and the surrounding Thiessen polygon area at three study sites in Yellowstone National Park. Analyses are for treatment plots in which no competitors had been removed and in which interspecific competitors had been removed.

No competitors removed:

	Site 7			Site 8			Site 11		
	r	P	n	r	P	n	r	P	n
Height	0.04	0.791	37	0.49	0.002	40	0.04	0.822	40
Diameter	0.15	0.355	37	0.58	<0.001	40	0.28	0.082	40

Interspecific Competitors Removed:

	Site 7			Site 8			Site 11		
	r	P	n	r	P	n	r	P	n
Height	0.25	0.120	37	0.30	0.057	40	0.11	0.498	40
Diameter	0.12	0.457	37	0.31	0.055	40	0.13	0.451	40

Table 16. Summary of correlation analyses between height or stem diameter of target *Pinus contorta* seedlings and summation of heights or stem diameters of potential conspecific competing neighbors identified as those defining the Thiessen polygon surrounding a target seedling. Analyses are for treatment plots in which no competitors had been removed and in which interspecific competitors had been removed.

Site	Target	No Competitors Removed				Interspecific Competitors Removed			
		Sum Height		Sum Diameter		Sum Height		Sum Diameter	
		r	P	r	P	r	P	r	P
7	Height	0.52	0.001	0.45	0.003	0.01	0.944	0.05	0.765
	Diameter	0.51	<0.001	0.45	0.003	0.03	0.854	0.30	0.068
8	Height	0.04	0.814	0.05	0.773	0.22	0.181	0.22	0.175
	Diameter	0.21	0.200	0.17	0.300	0.26	0.099	0.26	0.067
11	Height	0.53	<0.001	0.35	0.027	0.67	<0.001	0.60	<0.001
	Diameter	0.25	0.120	0.26	0.110	0.45	0.004	0.45	0.005

YELLOWSTONE NATIONAL PARK



Figure 1. Location of 12 study sites in Yellowstone National Park. Dark lines are major Park highways; large lakes are shown as black areas.

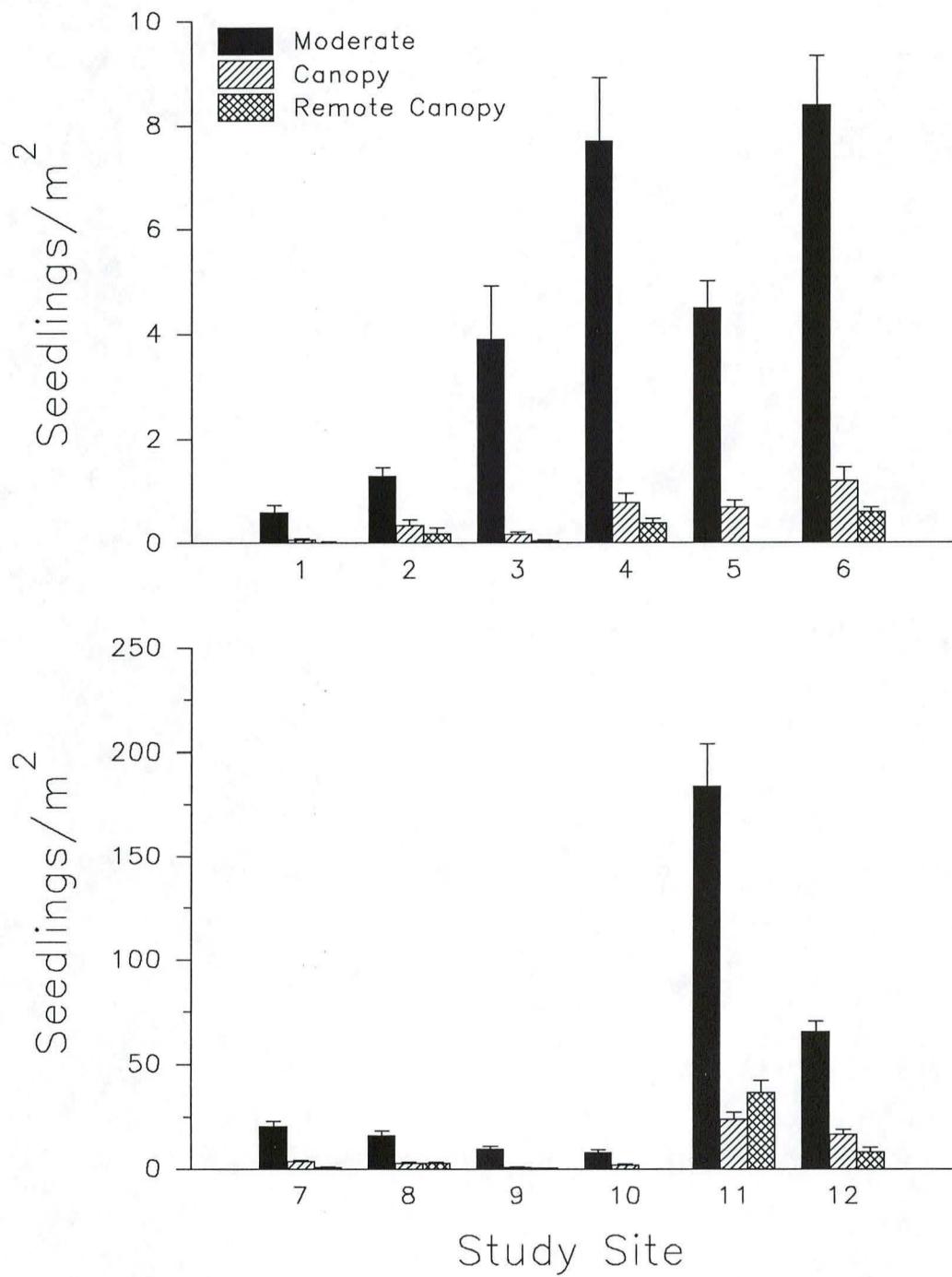


Figure 2. Mean densities of *Pinus contorta* seedlings in moderate, canopy, and remote canopy burn plots at 12 study sites in Yellowstone National Park in 1990 from areas burned in 1988. Error bars represent one standard error.

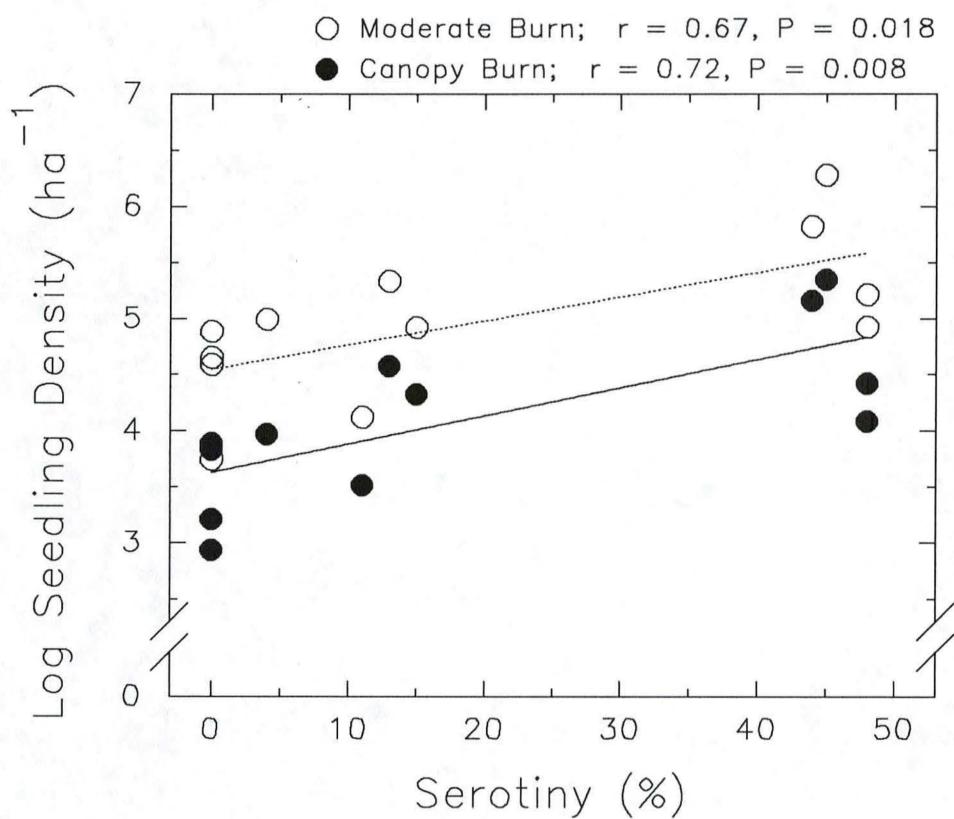


Figure 3. Correlation between log density of *Pinus contorta* seedlings in moderate or canopy burn plots and the proportion of trees in the adjacent unburned stand for 12 study sites in Yellowstone National Park. All data are from 1990.

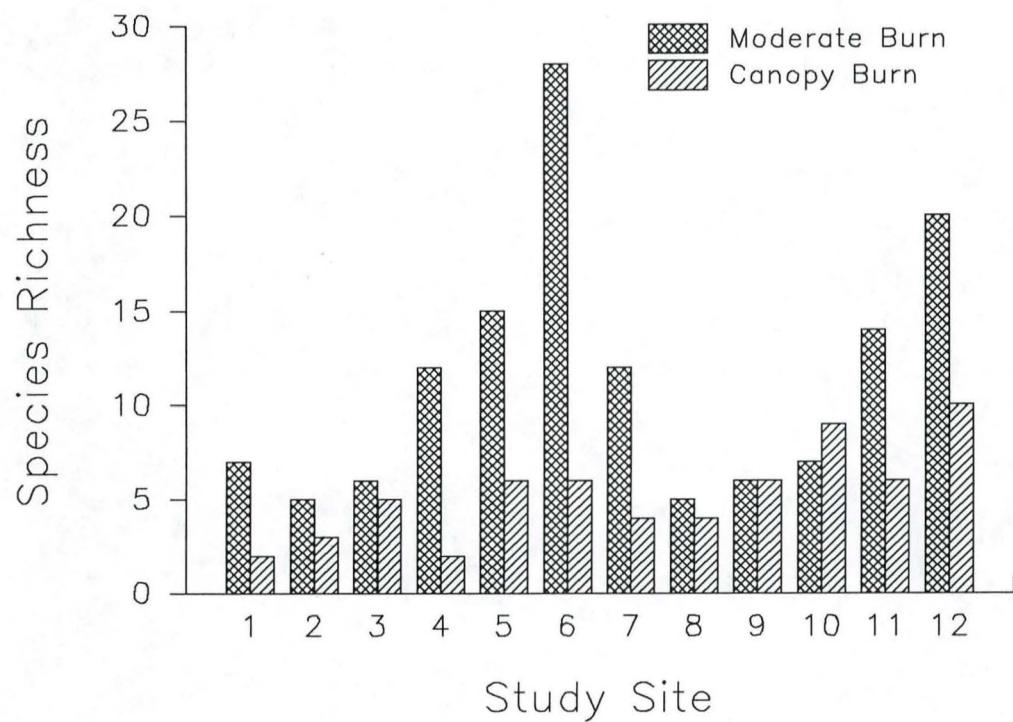


Figure 4. Richness of vascular plant species in moderate and canopy burn plots at 12 study sites in Yellowstone National Park. Data were taken in 1990 from areas burned in 1988.

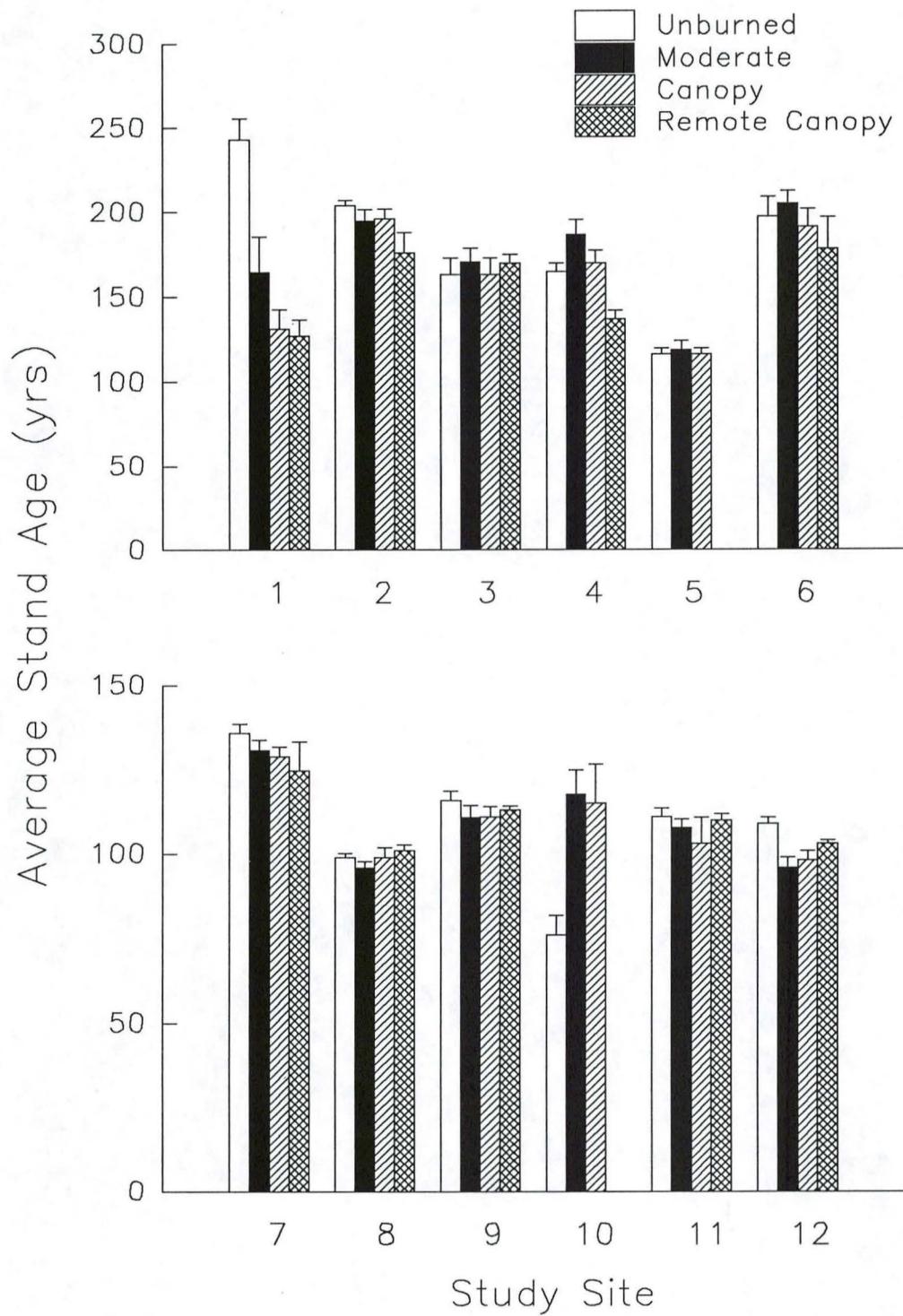


Figure 5. Mean age of 10 canopy-dominant *Pinus contorta* trees in unburned, moderate burn, canopy burn, and remote canopy burn plots at 12 study sites in Yellowstone National Park. Data were taken in 1990 from areas burned in 1988. Error bars represent one standard error.

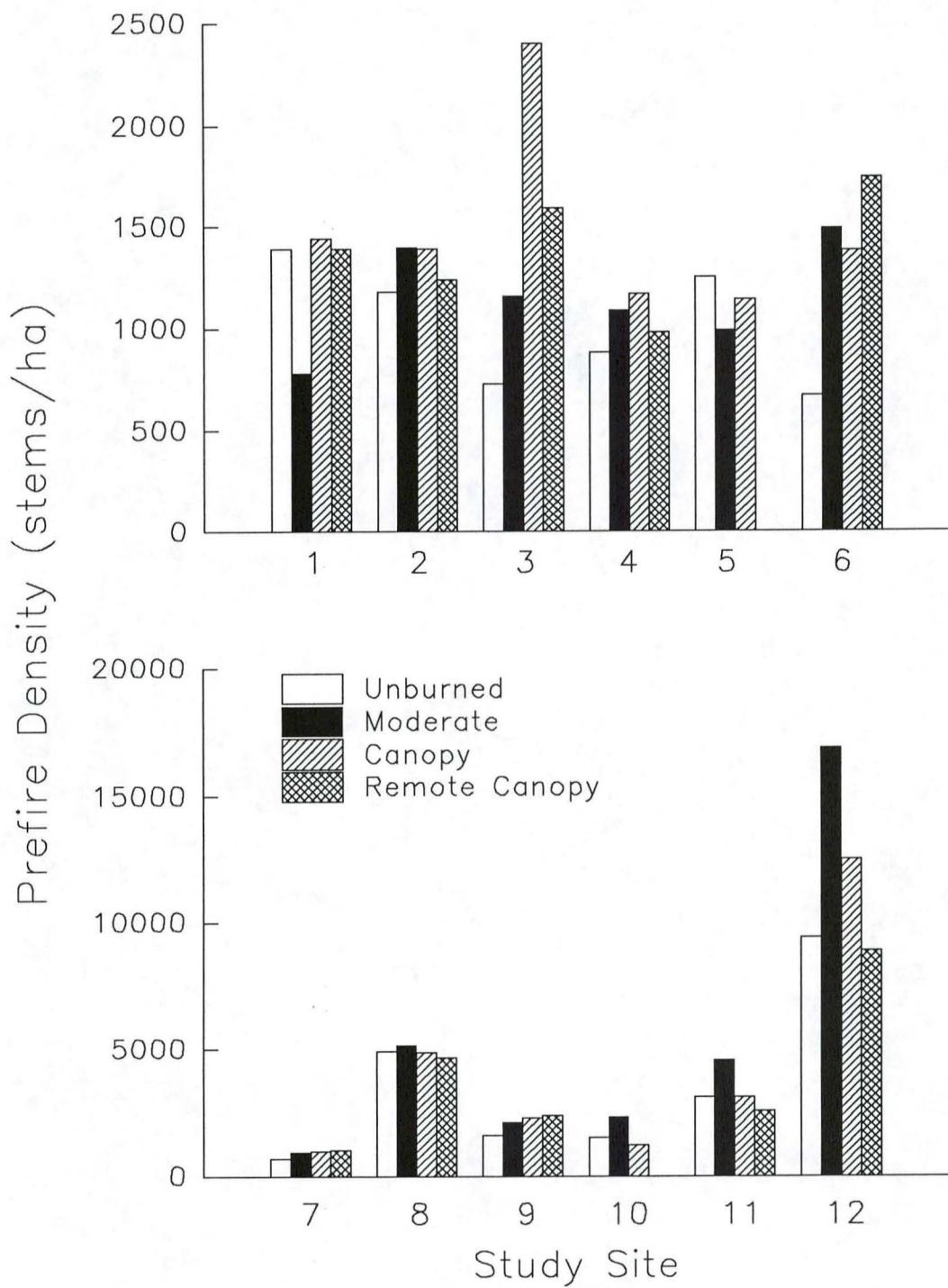
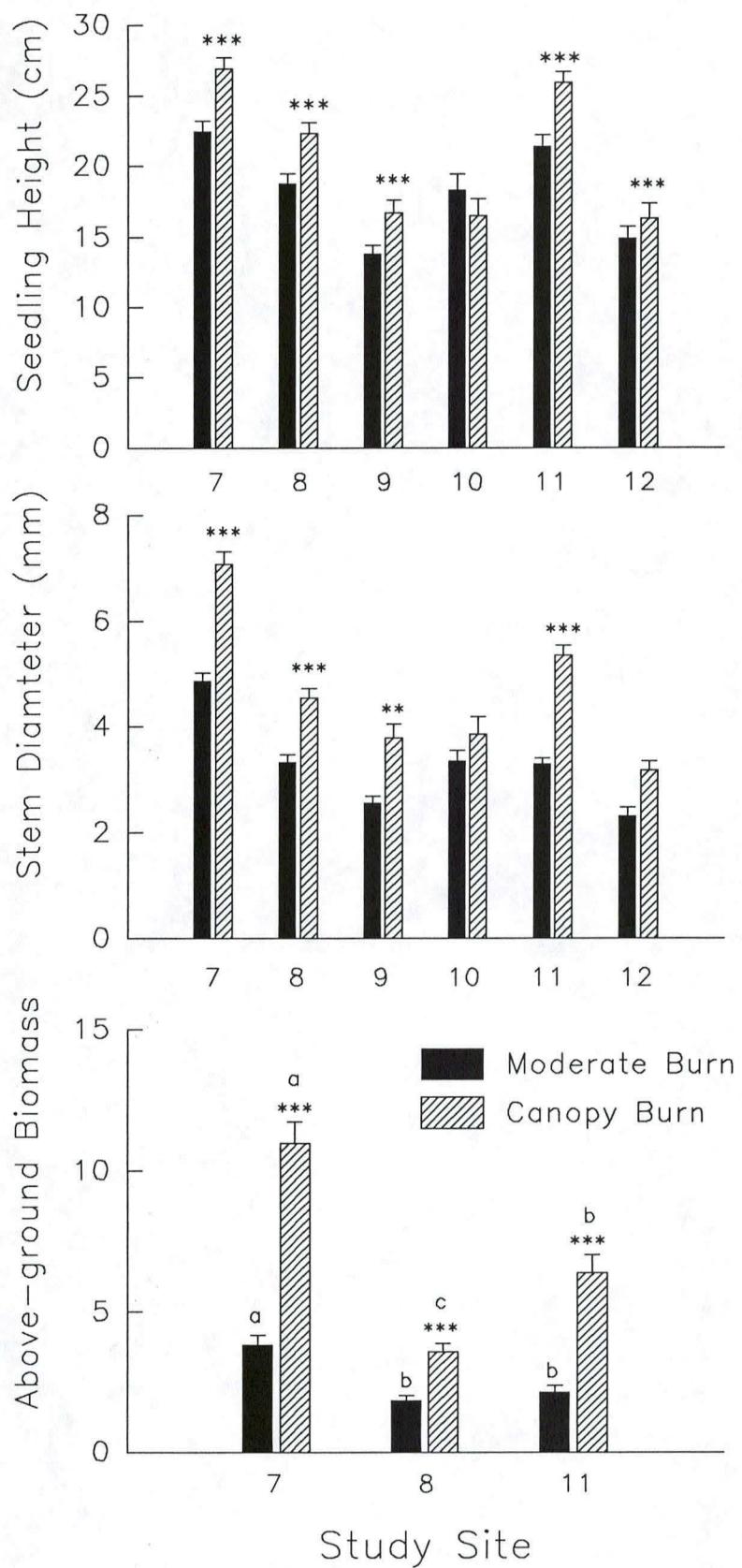


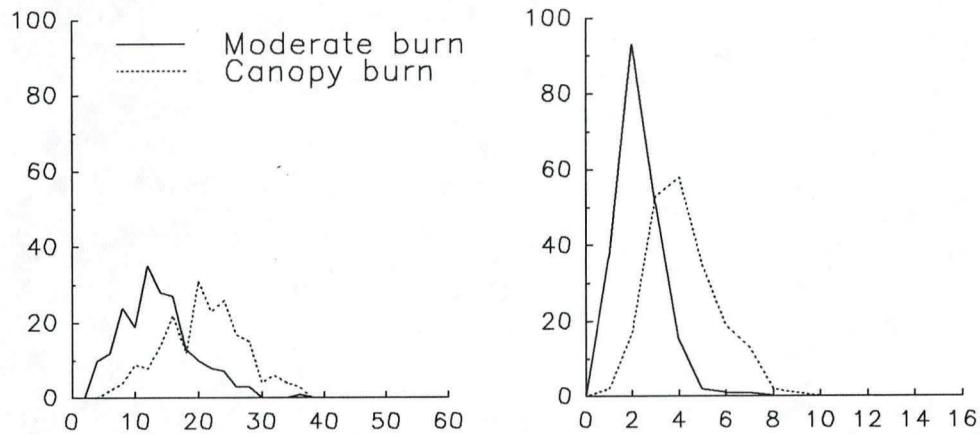
Figure 6. Prefire density of mature *Pinus contorta* trees in unburned, moderate burn, canopy burn, and remote canopy burn plots at 12 study sites in Yellowstone National Park. Data were taken in 1990 from areas burned in 1988.

Figure 7. Mean seedling height (top) or stem diameter (center) at five sites, and mean seedling above-ground biomass at three sites (bottom) in moderate and canopy burn plots. Error bars represent one standard error. Asterisks indicate a significant difference between the moderate and canopy burn plots at a particular site ($** = P < 0.01$; $*** = P < 0.001$). In the bottom graph, results of across site comparisons using Student-Newman-Keuls multiple range test are indicated with lower case letters. Means within a burn category associated with different letters are significantly different at $P = 0.05$. Data were taken in 1991 from areas burned in 1988.

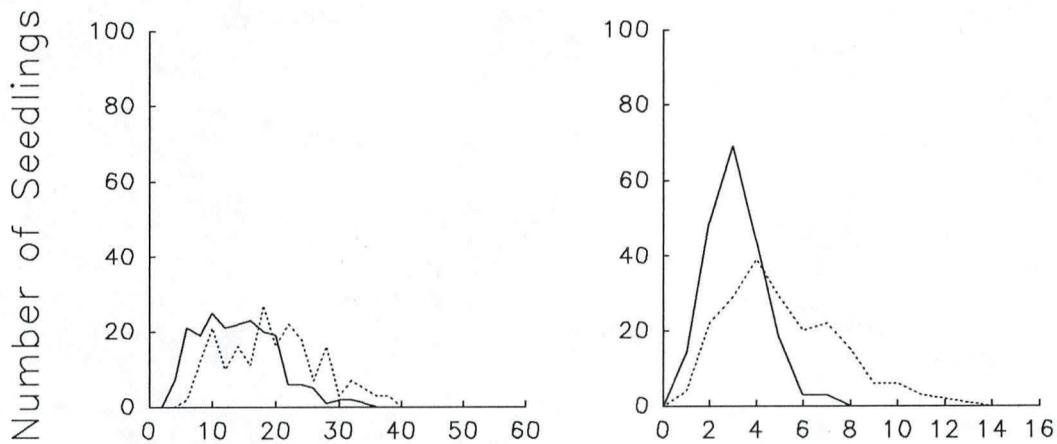
Figure 7



Site 11: Madison River Bridge



Site 9: Norris Junction South



Site 7: Swan Lake Flat

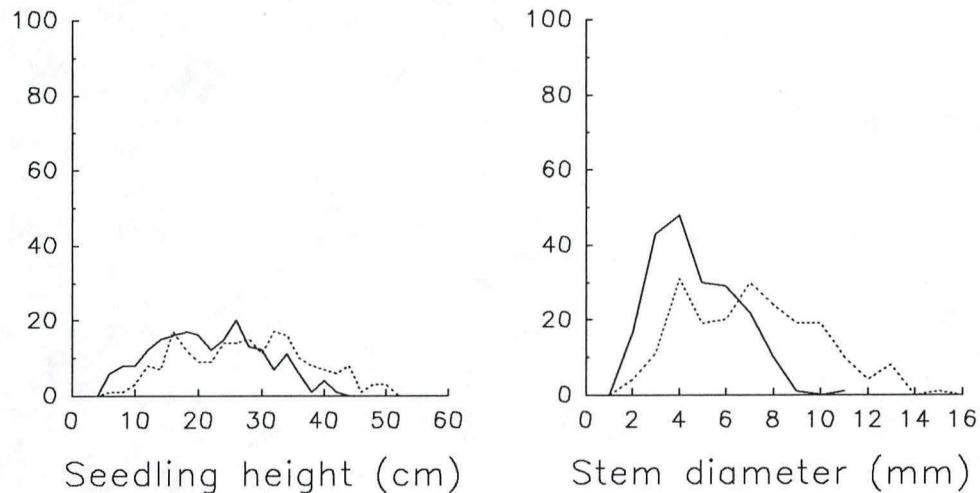


Figure 8. Frequency polygons for *Pinus contorta* seedling height and stem diameter at three study sites in Yellowstone National Park. Data were taken in 1992 from areas burned in 1988.

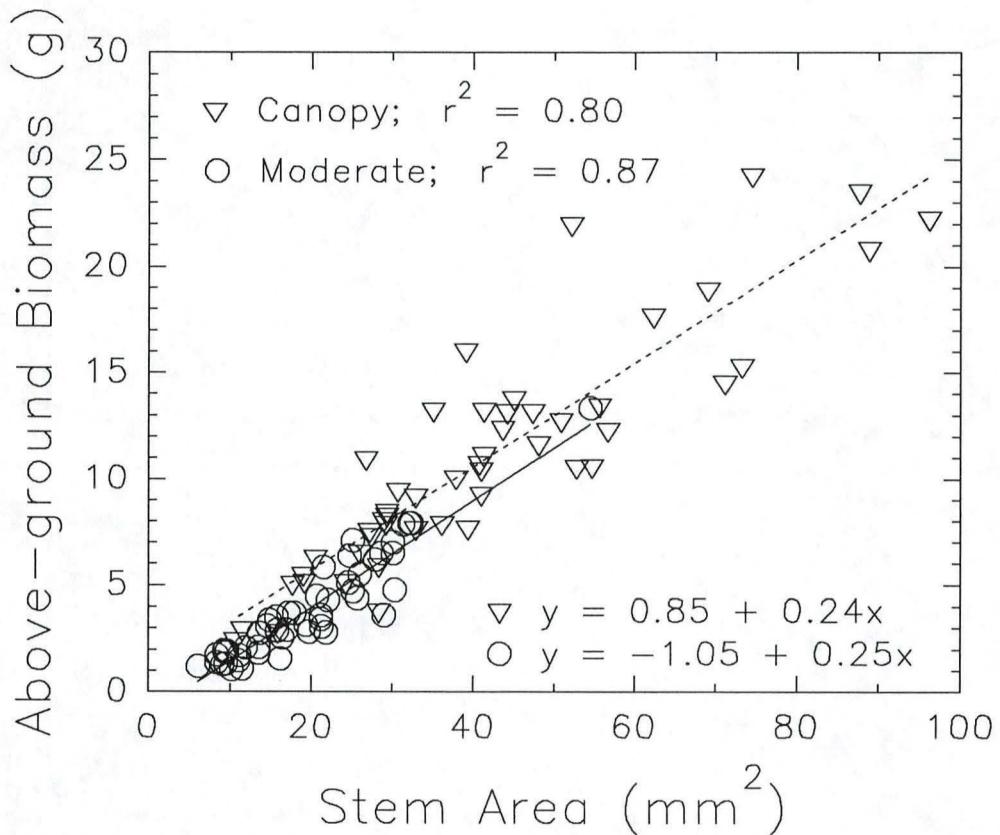
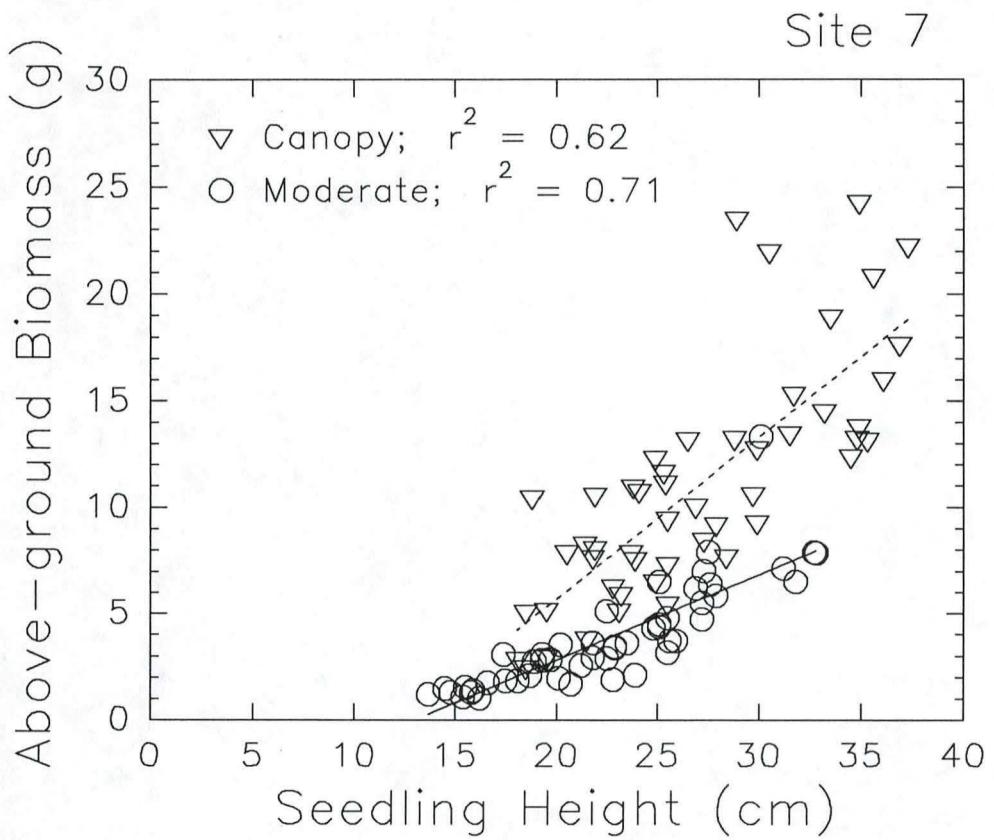


Figure 9. Relationship between above-ground biomass and *Pinus contorta* seedling height or cross-sectional stem area for moderate and canopy burn plots at study Site 7. Data were taken in 1991 from areas burned in 1988.

Site 8

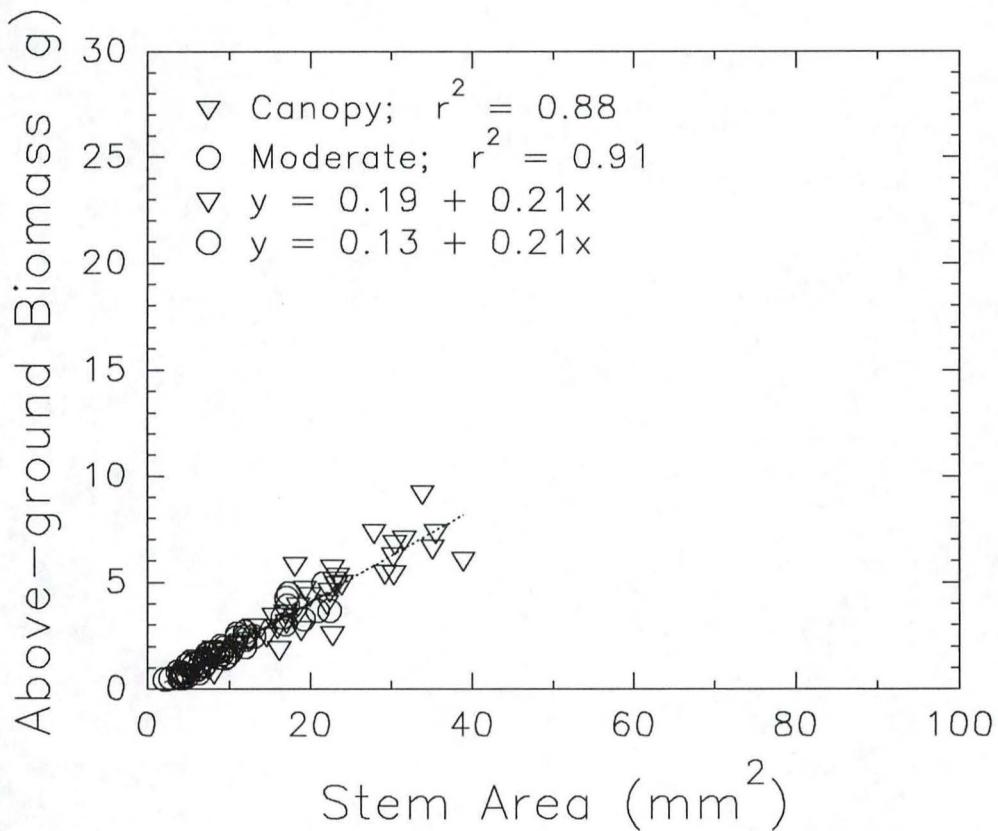
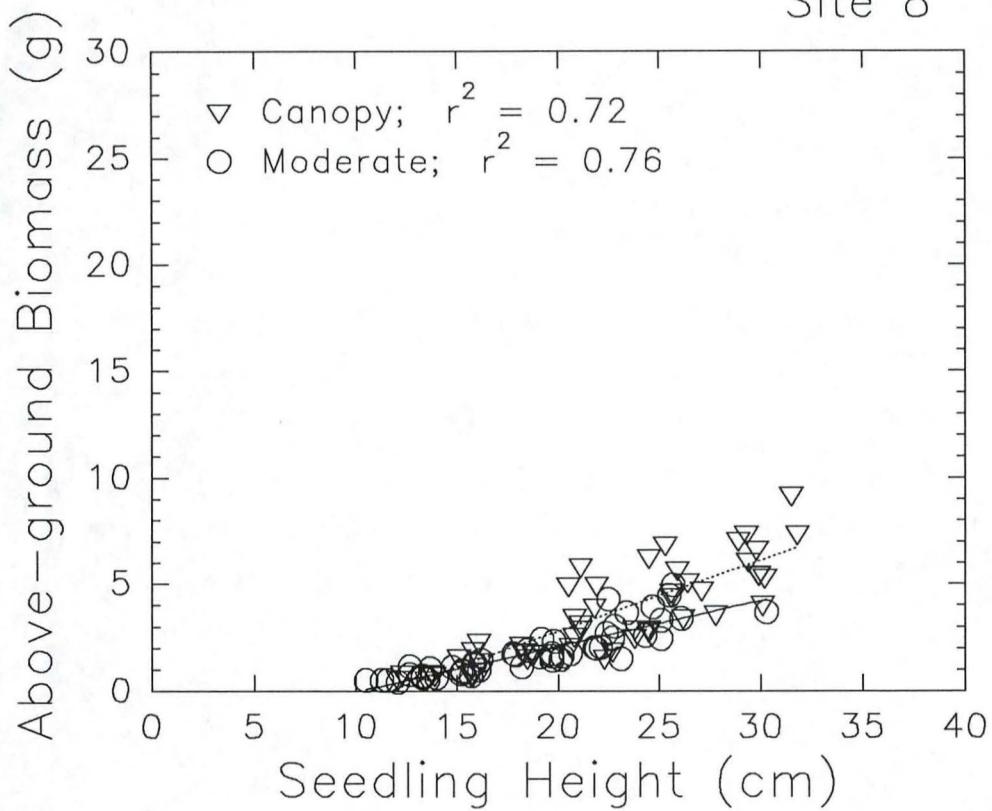


Figure 10. Relationship between above-ground biomass and *Pinus contorta* seedling height or cross-sectional stem area for moderate and canopy burn plots at study Site 8. Data were taken in 1991 from areas burned in 1988.

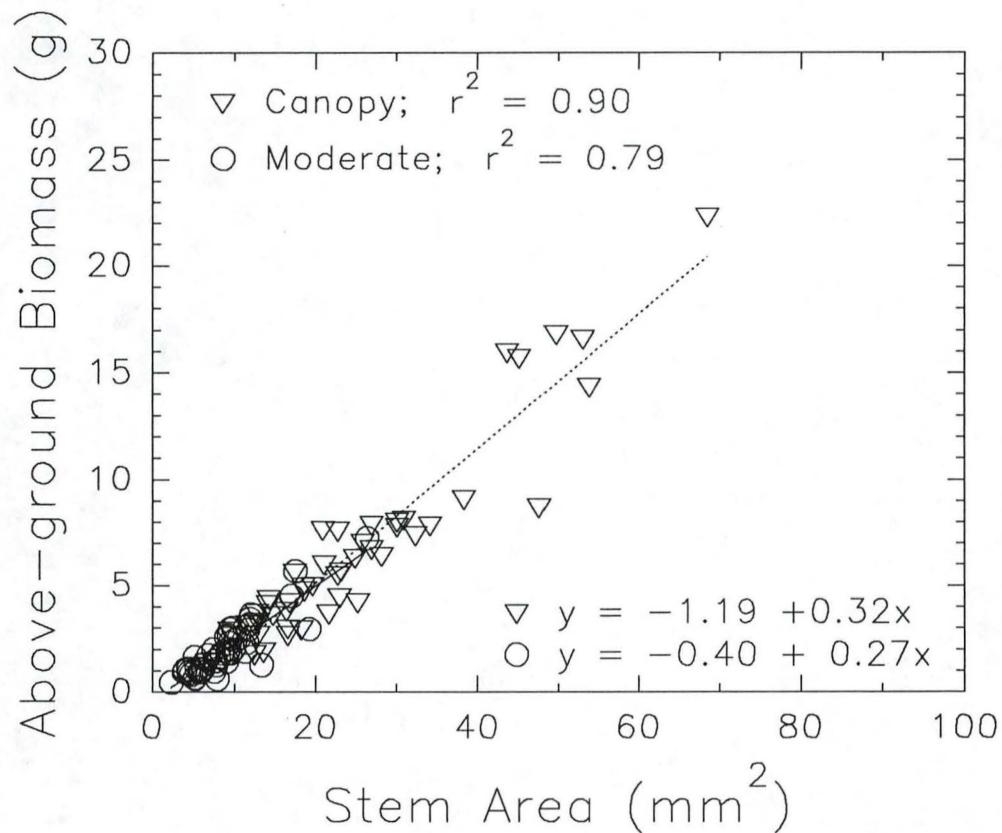
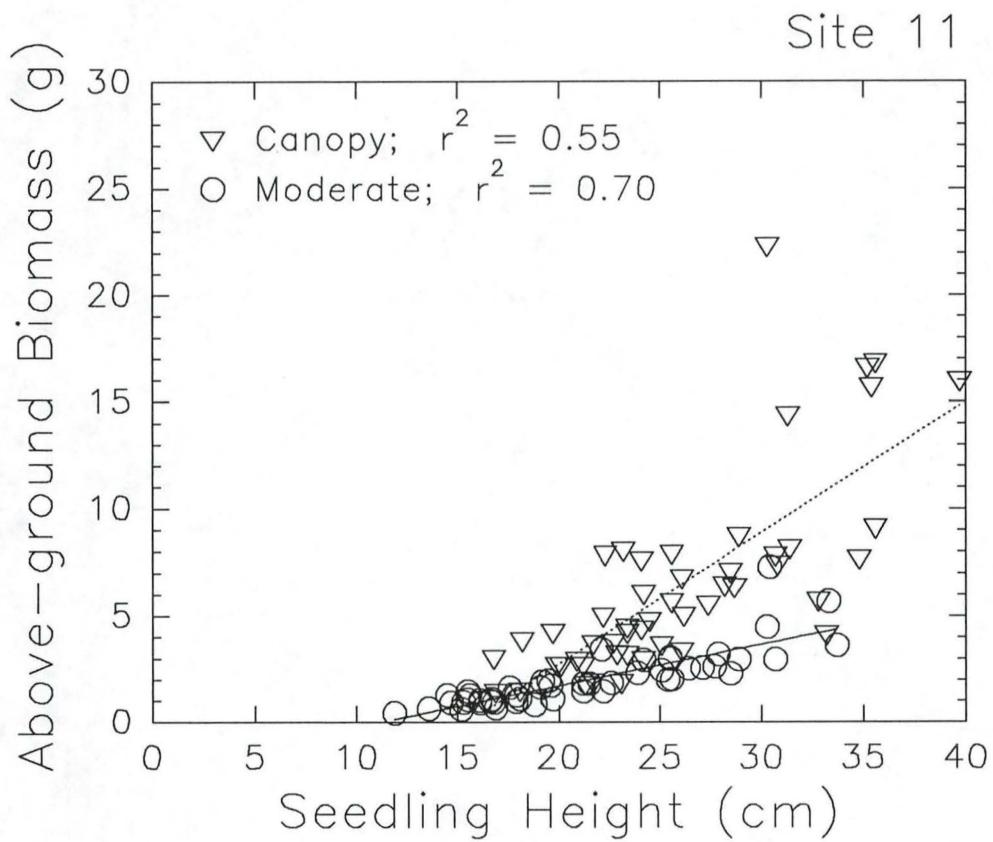


Figure 11. Relationship between above-ground biomass and *Pinus contorta* seedling height or cross-sectional stem area for moderate and canopy burn plots at study Site 11. Data were taken in 1991 from areas burned in 1988.

Site 7 – Swan Lake Flat

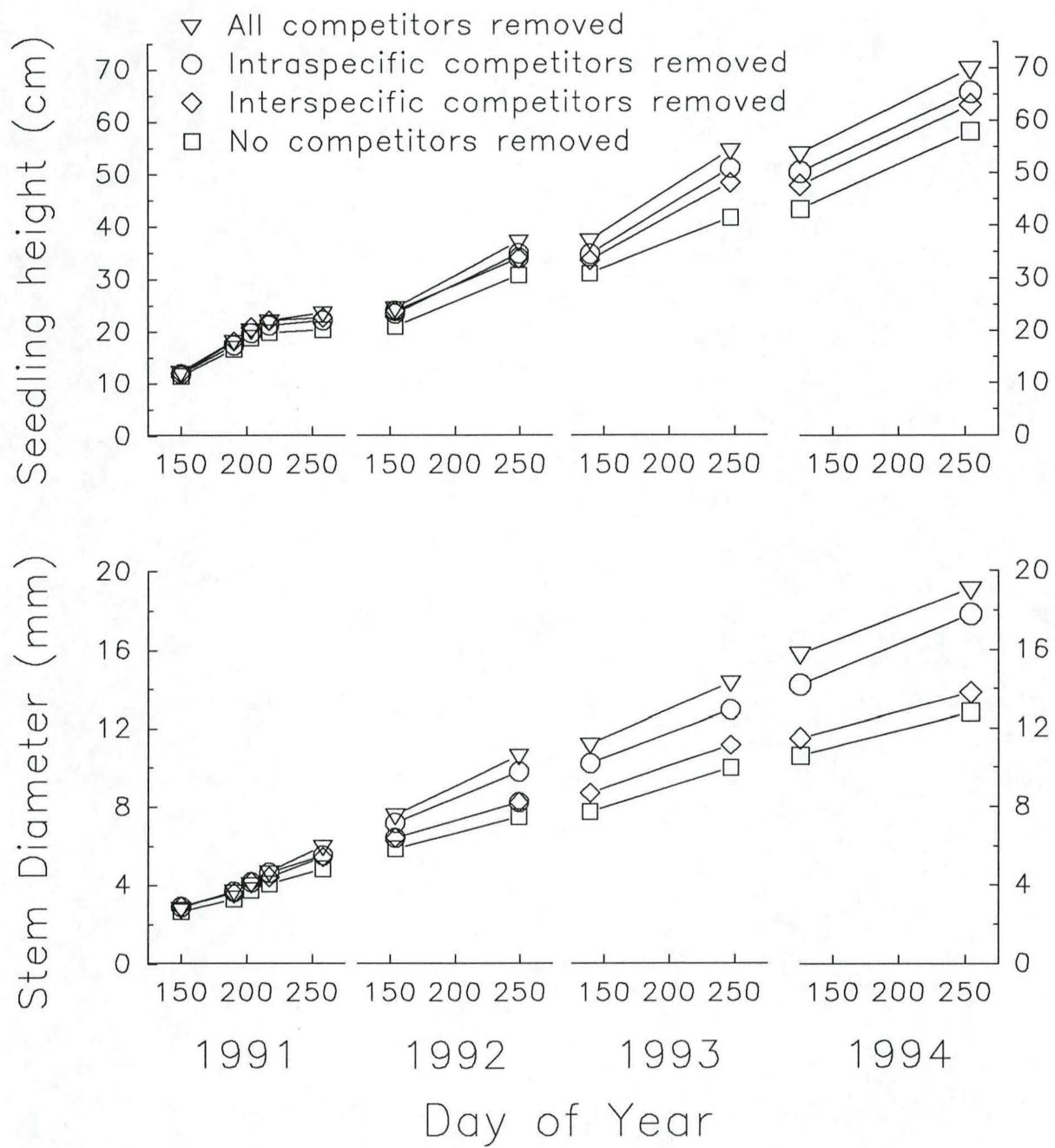


Figure 12. Effects of removing all, intraspecific, interspecific, or no competitors on height and stem diameter of target *Pinus contorta* seedlings at Site 7. See Tables 10a and 10b for statistical analyses.

Site 8 – Whiskey Flat

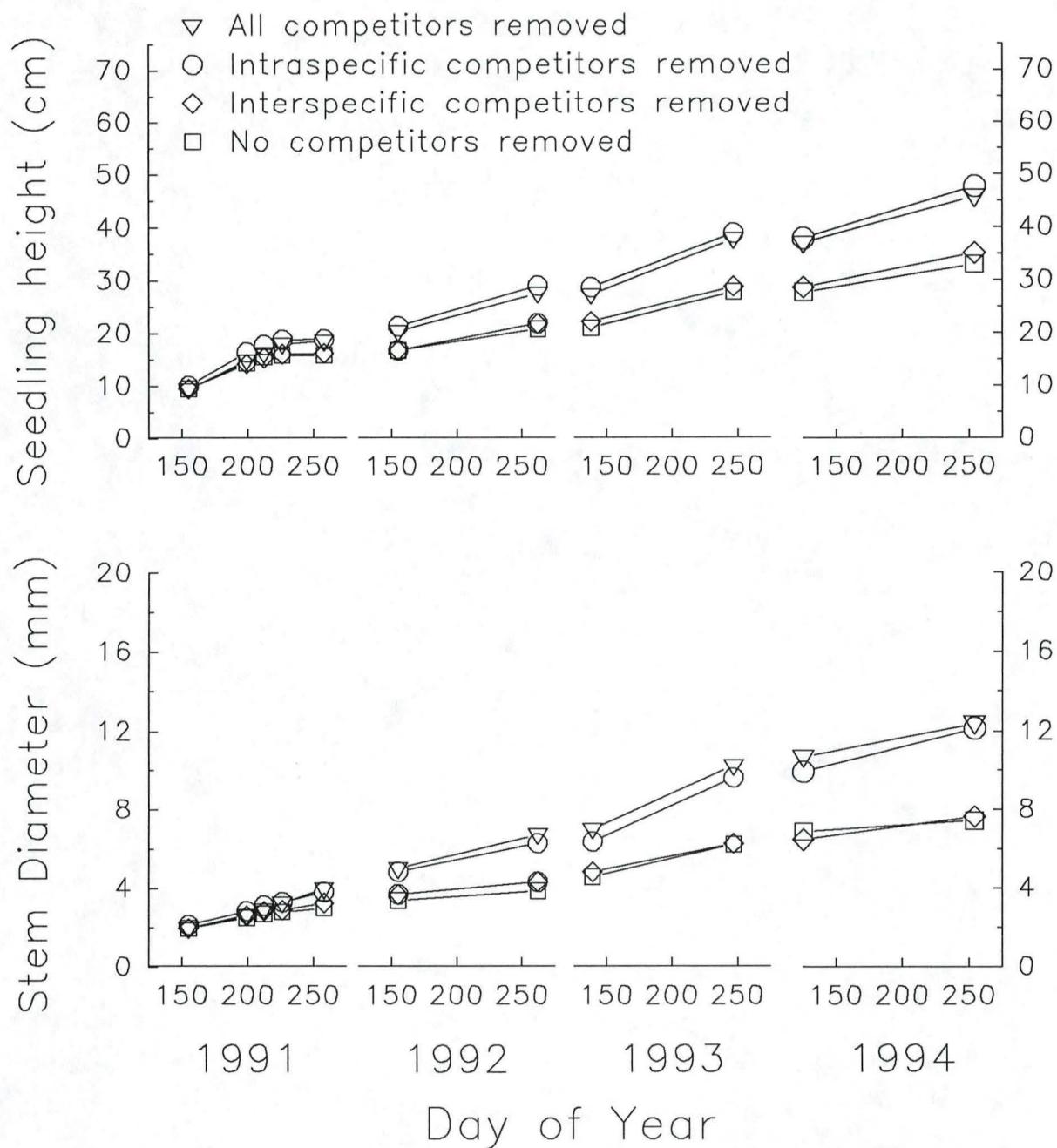


Figure 13. Effects of removing all, intraspecific, interspecific, or no competitors on height and stem diameter of target *Pinus contorta* seedlings at Site 8. See Tables 11a and 11b for statistical analyses.

Site 11 – Madison River Bridge

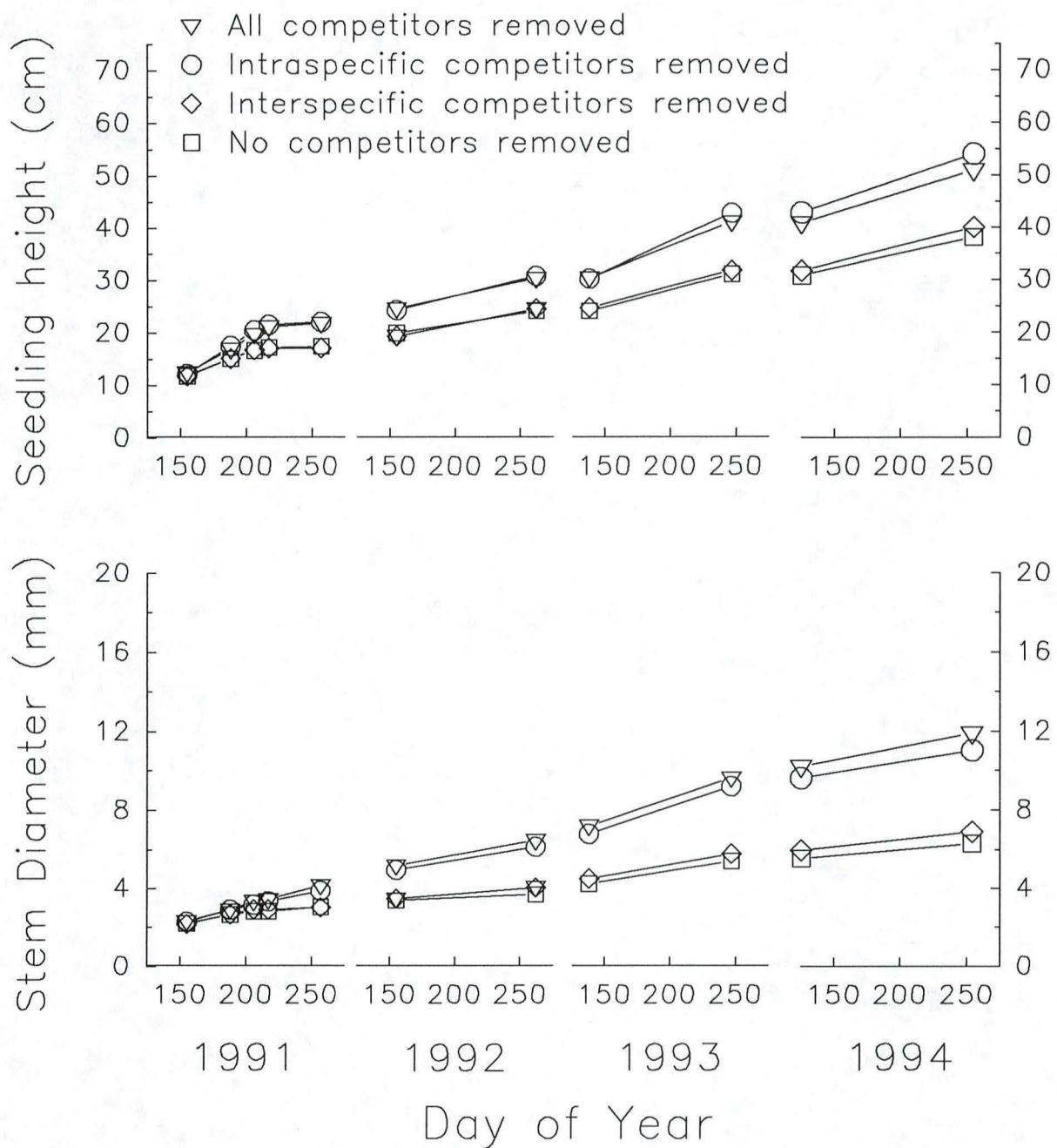


Figure 14. Effects of removing all, intraspecific, interspecific, or no competitors on height and stem diameter of target *Pinus contorta* seedlings at Site 11. See Tables 12a and 12b for statistical analyses.

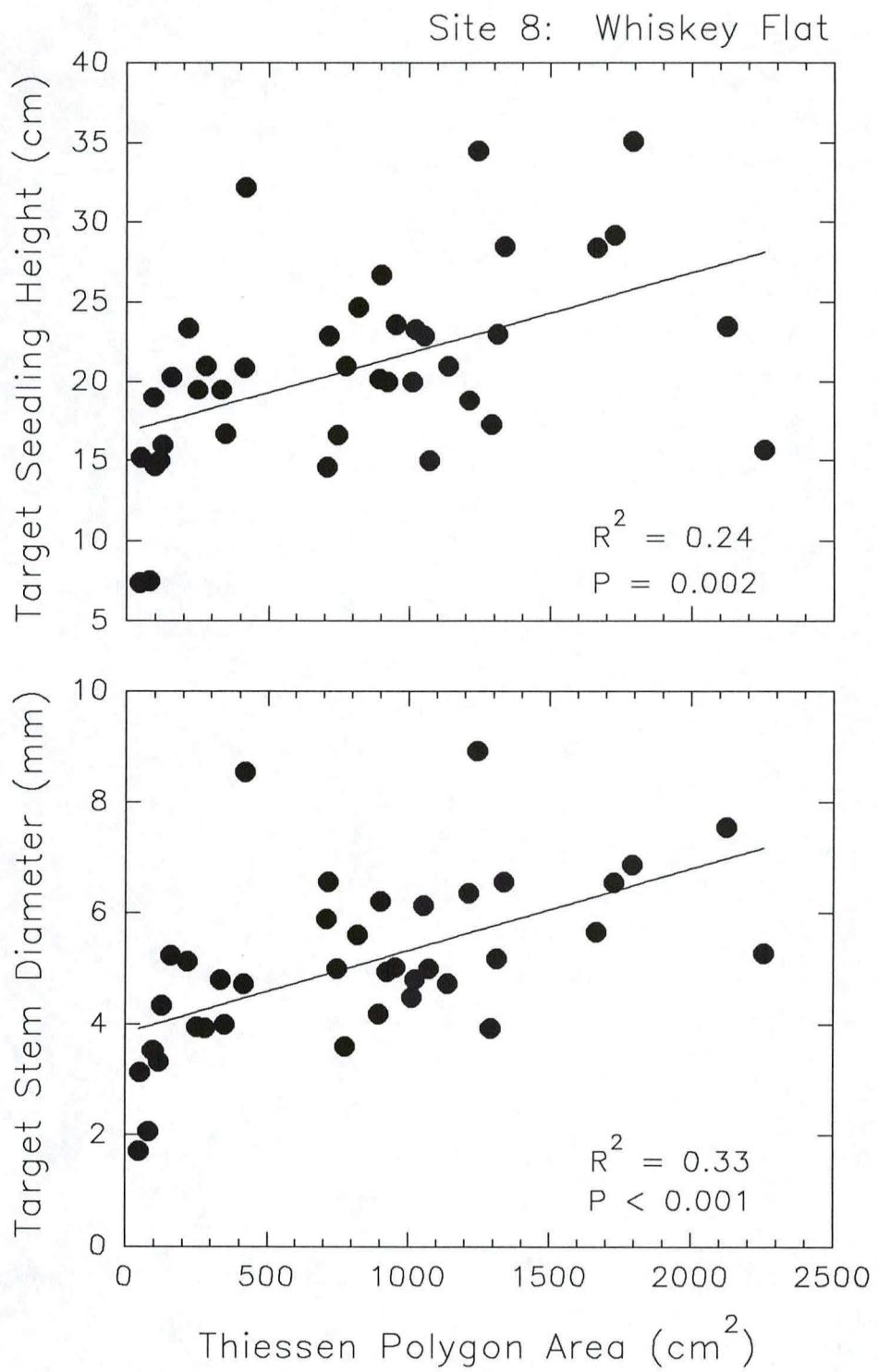


Figure 15. Relationship between height or stem diameter of target *Pinus contorta* seedlings and "available area" as estimated with Thiessen polygons (see Methods for details) at Site 8. Data are from treatment plots in which no competitors had been removed (see Table 15).

Site 7: Swan Lake Flat

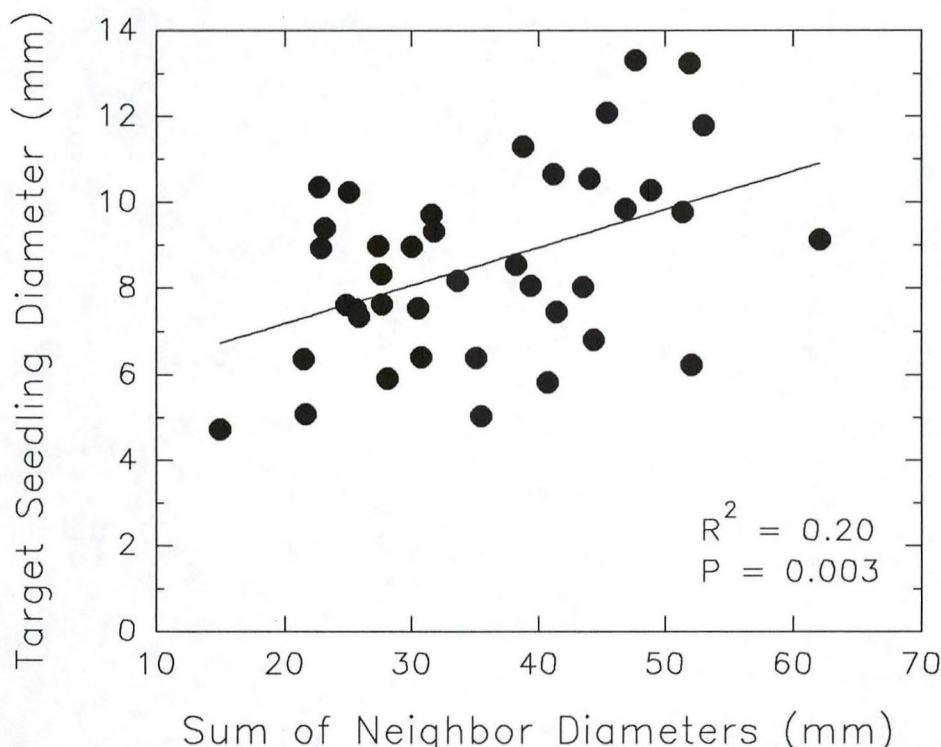
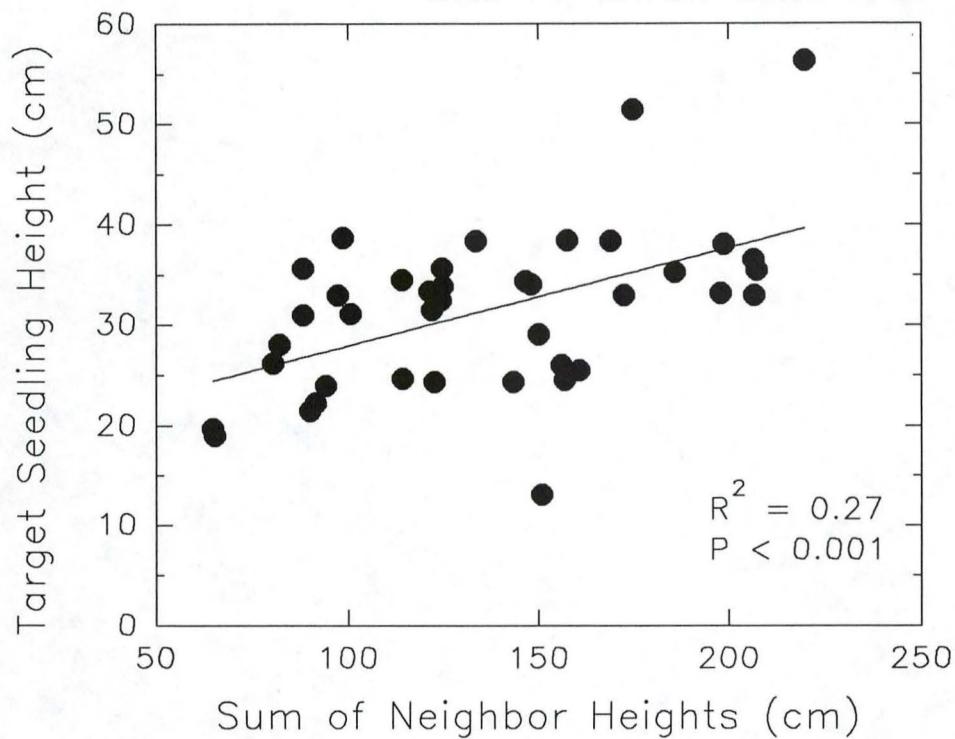


Figure 16. Correlation between height or stem diameter of target *Pinus contorta* seedlings and the sum of neighbor heights or neighbor stem diameters at Site 7. Neighbors were identified as those defining the Thiessen polygon around a target seedling (see Methods for details). Data are from treatment plots in which no competitors had been removed (see Table 16).